VOCAL COMMUNICATION IN AN INTRODUCED COLONY OF FERAL RHESUS MONKEYS (*MACACA MULATTA*)

By

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A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL
OF THE UNIVERSITY OF FLORIDA IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1983

I would like to dedicate this dissertation to my mother, Theresa Peters, and the memory of my late father, Paul Peters. Without their love and support, this dissertation could not have been written.

ACKNOWLEDGEMENTS

Every dissertation is the product of effort by many people, in addition to the author. Dr. William R. Maples chaired my committee and has been a continuing source of valuable advice. Drs. John H. Kaufmann, Leslie S. Lieberman, and Allan F. Burns also served on my committee and made many helpful suggestions. Drs. John G. Robinson and Linda D. Wolfe gave me the benefit of their varied experience as field primatologists. Dr. Anthony Holbrook of the Florida State University Speech Science Laboratory allowed me to use his equipment for the vocalization analysis and provided important technical assistance.

For permission to work on land owned by the American Broadcasting Companies, Inc. I am grateful to Tom Cavanaugh, General Manager of the Silver Springs attraction. Jim Lowry, Director of Operations, extended many courtesies to me during the data collection phase of this study and the entire staff of the Silver Springs complex have shared with me their observations, their ideas and their interest in this project. This research was supported by the Florida State Museum and a University of Florida Graduate School Fellowship. I am especially indebted to Drs. Maples and Kaufmann for guiding me to these funding sources.

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April, 1983

Chairman: William R. Maples
Major Department: Anthropology

Vocal communication in a free-ranging group of rhesus monkeys (Macaca mulatta) was examined in order to provide baseline data on the social use of vocalizations in a complex environment. The subjects were a natural troop of feral monkeys inhabiting the banks of the Silver River near Silver Springs, Florida.

Vocalizations were recorded and accompanying behavioral data collected using both ad libitum and sequence sampling. Spectrograms were made of representative vocalizations and a catalogue was constructed delineating both the physical characteristics of the sounds and their social usage. Functional, as well as acoustic, criteria were used to distinguish calls, analogous to the manner in which phonemes are distinguished. The present catalogue was compared with other catalogues previously published for rhesus monkeys and other species of macaque.

Both the stereotypy of some calls and the graded nature of other calls were noted. It was suggested that all calls could best be understood as the result of position along a series of form gradients, with stereotypic calls occupying relatively invariant positions and "graded" calls occupying variable positions along one or more gradients. The possibility that meaning may be the result of position along multiple form-meaning gradients was also suggested as a constrast to the standard assumption that meaning is categorically coded.

Evidence for individualization was examined for the call designated the "basic coo." Although usually referred to as a contact call, the individualized nature of this call suggests that it may function to provide a maintenance level of individualized interaction between group members, necessary to inhibit xenophobic aggression within the group.

CHAPTER I

THE STUDY OF VOCAL-AUDITORY COMMUNICATION IN THE RHESUS MONKEY

Sociality has both advantages and disadvantages and only a limited number of animal taxa have evolved a social way of life. Once evolved, however, sociality has consequences for the nature of future selection pressures on a species. One of the correlates of sociality seems to be an increase in the amount of information transferred between conspecifics and one can perhaps best gauge the degree of sociality of a species by the scope, complexity and effectiveness of its conspecific communication system.

Humans and many species of non-human primates have evolved elaborate conspecific interdependencies mediated by equally elaborate communication systems. Of the multiple channels by which information might be transferred (including chemical, tactile, auditory, and visual), it should not surprise us that socially living primates seem to make use of all of them. Among humans, however, one modality--the auditory--has come to predominate. Although humans stand alone in the evolution of a linguistic system, we are not alone in the use of the auditory channel for information transfer. Investigating the degree to which closely related non-human species have also accessed its possibilities can be useful for two reasons. First, we need to understand the contribution which auditory information makes to the

construction and maintenance of species-typical social relations. Kummer (1971) has suggested that the proximate causes of social organization are still poorly understood and it seems to be equally true that the role which vocal communication plays in the construction and maintenance of social relationships has not been appreciated. Second, it is only after investigating _what_ information is transferred in this channel in closely related species (and _how_ this information is transferred) that we can accurately specify the emergent functions of human language and reconstruct the evolutionary sequence which led to linguistic coding.

The present study is an investigation of the vocal-auditory communication system of the rhesus monkey. This animal has probably been the object of more scientific research than any other primate species save our own. Considering the magnitude of the data base which has been accumulated about its behavior as well as its physiology, surprisingly little has been documented about spontaneous vocal communication, particularly in free-ranging animals. A major objective of the present study has been to remedy this deficit by describing the social use of vocalization in a natural group of feral animals.

The subjects of this study are themselves interesting and unique. They are a natural troop of free-ranging rhesus monkeys inhabiting the banks of the Silver River near Silver Springs, Florida. They are part of a colony of approximately 200 animals which is reputed to be descended from a small number of imported monkeys released into the wild during the filming of a commercial movie in the 1930s. The successful accommodation of these

introduced animals to this Florida habitat is itself a phenomenon of some interest and the description of their vocal behavior is part of this story.

The Silver Springs monkeys are presented with complex social and physical challenges at the same time that they are provided with an opportunity to respond to these stimuli in species-typical social style. The description of vocal communication in these animals should provide useful baseline data on relatively normal social behavior against which the vocal behavior of laboratory animals (under varying regimens of stimulus control) can be compared. Additionally, as the vocal behavior of free-ranging rhesus monkeys (and other macaque species) at other geographic locations continues to be investigated, the broader range of stimuli and responses associated with each call can be considered when inferring the probable meaning of the call.

A secondary objective of the present report (and one which suggested itself only after data collection had been completed) has been to examine the evidence for individualization in one of the calls frequently emitted by these study animals. Individualization in sound signals has received very little attention by primatologists yet individualized behavior is a basic feature of the social behavior of higher vertebrates. It should be of some interest, therefore, in our assessment of how calls function, to determine whether sound signals convey information about the identity of the caller. While the analysis contained in this report is limited, it is offered as an inducement to further study of this phenomenon.

Earlier Investigations of Rhesus Vocal-Auditory Communication

"The first step in any analysis of vocal behavior must be the development of reliable descriptions of the sounds. Despite the widespread use of the rhesus monkey as a subject of scientific inquiry, successful attempts at describing the vocal behavior of this species have been surprisingly few . . ." (Erwin, 1975). This state of affairs has not changed since 1975. Although social communication in the rhesus monkey has been the subject of scientific inquiry for more than two decades, the description, classification, and understanding of the sound signals used by these animals is still at a very preliminary stage.

Since rhesus monkeys have a long history as laboratory research subjects, references to specific vocalizations made by captive animals appeared quite early in the scientific literature (e.g., Lashley and Watson, 1913; Foley, 1934). However, the first systematic attempts to describe the total vocal repertoire of this species were part of a more general concern with analyzing the full range of species-typical behavior into component units, the necessary first step to any elucidation of structure or pattern in behavior.

In 1956, Chance published his study of a colony of rhesus monkeys at the London Zoo. He defined 21 categories of social behavior including four kinds of vocalization. Both the classification of the sounds and the description of sound structure were crude by contemporary standards. The vocalizations were given onomatopoetic labels using English alphabetic letters (e.g., "Eeech"), a method which can only communicate gross features

of the animal sound and which biases the observer to attend to those acoustic features which are similar to English sounds. Despite its limitations, this study represents a pioneering attempt to distill from the ongoing behavioral stream of a non-human primate the repetitive categorical units of vocal and general motor behavior.

A somewhat more detailed analysis of the behavior of a captive group of rhesus monkeys located at the Whipsnade Zoo Park was published by Reynolds (1961, quoted in 1976), a student of Chance. Among his behavioral categories, he distinguished 11 "vocal units" to each of which he assigned a descriptive name (e.g., "explosive cough"). Although many of the same classification and description problems which Chance encountered also attended the Reynolds study, the latter investigation does show an increase in attention to subtle differences in context and acoustic structure for defining sound units, with a resultant increase in the differentiation of units.

An independent analysis of the communicative behavior of the rhesus monkey was carried out by Altmann (1962, 1965, 1968) following two years of study of the monkeys of Cayo Santiago. This investigator had the advantage over the earlier researchers of working with a large group of free-ranging animals responding to a much more complex set of physical and social stimuli.

Altmann's goal was a "complete catalogue of mutually exclusive, socially significant behavior patterns" (1962, p. 373). He defined 59 classes of single patterns (and a slightly greater number of multiple patterns) including seven vocalizations which he characterized through the use of the International Phonetic Alphabet. These seven vocalizations were gleaned

from "a working list of 17 vocalizations" after variability which he attributed to differences in age, sex, motivational intensity, and social context of the vocalizing animal were eliminated. Although Altmann had tape recordings of the monkey's vocalizations, his ability to classify and describe these sounds were constained by a number of factors. First, since he sorted sounds by ear, he was dependent on (and limited by) his own auditory perceptual and processing abilities for detecting differences in acoustic structure. Second, the standardized descriptive terminology which he used was developed for human linguistic sounds and since monkeys can make sounds which have no human equivalent, this terminology cannot adequately convey actual sound structure. It may also predispose an investigator to ignore species-specific sound distinctions which have meaning for the animal. Finally, Altmann had a methodological commitment to distinguish vocal categories by acoustic structure only, without reference to the context in which the sound was used (cf. Marler, 1965). This resulted in his merging into a single category sounds which occurred in very different contexts simply because they sounded similar to the human ear and it meant that contextual cues which might make a significant contribution to the meaning of a sound signal were ignored. As a consequence of these problems and restrictions, it was Altmann's own assessment that both the classification and description of vocalizations were "unsatisfactory" and represented one of the "shortcomings" of his final behavioral catalogue (1962, pp. 380-381).

The description of the physical structure of animal sounds entered a new era of precision and reliability with the introduction of spectrographic analysis of sound recordings (Koenig, Dunn and Lacey, 1946). This technique

provides a graphic representation of a sound, making it possible to sort and describe sound signals by visual examination and by relatively precise measurements of the frequency-temporal-intensity patterning of the sound. First used for the analysis of birdsong (Borror and Reese, 1953), sound spectrography was later applied by Rowell and Hinde (1962; also Rowell, 1962) and by Andrew (1962, 1963) to the vocalizations of non-human primates. The vocalizations of rhesus monkeys were among the first to be analyzed with this new technique although it was soon applied to the analysis of the vocal repertoires of a wide range of non-human primate species including guenons (Chalmers, 1963; Struhsaker, 1967; Gautier, 1978), squirrel monkeys (Winter et al., 1966), gorillas (Schaller, 1963; Fossey, 1972), langurs (Vogel, 1973), tamarins (Moody and Menzel, 1976), howler monkeys (Baldwin and Baldwin, 1976), lemurs (Pailette and Petter, 1978), colobus monkeys (Walek, 1978) and titi monkeys (Robinson, 1979).

Andrew (1962, 1963) was mainly concerned with showing the evolutionary sequence by which protective responses could give rise to the variety of calls and facial expressions evident across the entire primate order. He published spectrograms and made comparisons among the vocalizations of 33 species of primates, including humans. Although he devoted only limited attention to rhesus vocalizations, he did distinguish six types of calls from recordings made of animals in unspecified "laboratory colonies." He gave a physical description of each call, published spectrograms of three variants of each of two of the calls, and made a preliminary attempt to relate these calls to published accounts of their use. The analysis of rhesus vocalizations is necessarily brief and superficial. Andrew's work is notable less for the rigor

of his treatment of any single species than as an early attempt to show systematic relationships among all primate calls and facial expressions.

The classic analysis of the vocal repertoire of a single non-human primate species was carried by Rowell and Hinde (1962) and by Rowell (1962) on 24 caged rhesus monkeys (housed in three social units) located at Madingley near Cambridge. These investigators presented in separate publications the results of their analyses of movement patterns and of vocalizations. While their catalogue of movement patterns (Hinde and Rowell, 1962) was not as extensive as Altmann's (1962, 1965, 1968), the catalogue of vocalizations was highly differentiated and has, in fact, become "the standard system for describing rhesus vocalizations" (Erwin, 1975, p. 366). The success of their system can be attributed mainly to their use of sound spectrograms to aid in the classification and description of the sound units, but it may also be due, in part, to their use of contextual information for sorting sounds.

Rowell and Hinde distinguished two main groups of sounds--harsh noises and clear calls. Within these broad classes, they identified 12 kinds of harsh vocalizations (8 agonistic sounds--later expanded to 9 in Rowell (1962)--and four "friendly" noises). Their ability to categorize clear calls was constrained by what seemed to be a higher degree of interindividual variability than was true of harsh noises, and the investigators limited themselves to giving examples of calls which occurred in five situations. In addition to presenting a catalogue of rhesus vocalizations which was more differentiated than any which had preceded it, the Rowell and Hinde (1962) study is notable for suggesting that the sound units in the rhesus repertoire grade into each other

with intermediates between the labeled sounds expressing intermediate motivational states. In a separate paper, Rowell (1962) showed how all of the labeled agnostic and defensive sounds of the rhesus repertoire could be arranged in a continuing series linked by intermediates.

Despite the importance of this classic early study, several limitations of the data become apparent upon closer examination. First, the study was conducted on captive animals with a consequent limitation on the range of stimuli to which the animals were exposed. As the authors themselves suggested (p. 294), sounds elicited by stimuli not found in captivity may remain to be discovered. The study of free-ranging animals may also supply more information about the range of situations in which each type of vocalization is given, thus providing more clues to the meaning of each sound. Second, although Rowell and Hinde (1962) and Rowell (1962) catalogued harsh noises, no comparable catalog of clear calls was made and this remains a major gap in our knowledge of the rhesus repertoire. Third, Rowell and Hinde focused on sounds given by adult animals and presented only limited information about sounds given by younger animals. In view of the extensive use of young rhesus monkeys in studies of social separation effects (see Mineka and Suomi, 1978; Rajecki et al., 1978; Akins, 1980 for reviews of this extensive literature), describing the use of these vocalizations in an undisturbed environment would seem to be of paramount importance. Finally, although Rowell and Hinde discuss the problem of variability in certain calls and the sorting difficulties which this variability presents (particularly for clear calls), they do not present any details about how they dealt with it. As a result, it is impossible to know whether they sorted spectrograms on the basis

of invariant features which distinguish call types across a large number of individuals or whether features specific to the calls of some individuals were inadvertently given excess weight. This problem will be taken up again in Chapter IV.

The most recent attempt to deal with the total vocal repertoire of the rhesus monkey was undertaken by Lindburg (1971) as part of a general descriptive study of forest-living rhesus monkeys in northern India. Although he did not record or spectrographically analyze the vocalizations of his study groups, Lindburg did use the categories and labels which Rowell and Hinde (1962; also Rowell 1962) established for harsh noises. This represents the first attempt to apply a broad range of Rowell and Hinde's spectrographically derived sound categories to free-ranging animals. The ease with which he was able to sort most vocalizations by ear once categorical labels and descriptions had been previously supplied suggests that categorical features may be more important to the functioning of these sound signals than the "gradedness" which has attracted so much attention. Lindburg introduced a sound category not established by Rowell and Hinde (the "squawk") and he made no mention of two of Rowell and Hinde's categories (the "roar" and the "long growl"), although it is not clear whether he did not hear these sounds or he submerged samples of these sounds into other categories. Lindburg also defined a broad category which he labeled "calls" (roughly homologous to Rowell and Hinde's "clear calls") and described five situations in which such sounds occurred and the variation in sound quality associated with these situations. The lack of spectrographic analysis was particularly unfortunate

in this latter category of sounds because they could not be easily equated with any previously published spectrograms.

Despite the early and promising start on the description and understanding of rhesus vocalizations which the above studies represent, there is a noteworthy deficit of any later investigations of the vocal repertoire. There have been continuing references to the use of vocalizations by captive animals, often with an attempt to measure the effect on vocal behavior of variables such as age (Manocha, 1968; Erwin and Mitchell, 1973), sex (Rowell and Hinde, 1963; Maple et al., 1973), parity (Mitchell and Stevens, 1969), hormonal state (Maple et al., 1974), rearing experience (Mitchell et al., 1967; Spencer-Booth and Hinde, 1971; Brandt et al., 1972; Stevens and Mitchell, 1972; Newman and Symmes, 1974), social stimulus (Mitchell et al., 1966; Willott and McDaniel, 1974) or more than one of the preceding factors (Cross and Harlow, 1965; Mitchell, 1968; Moller et al., 1968; Baysinger et al., 1972; Maple et al., 1975). There have also been attempts to specify the features of the rhesus brain (Robinson, 1967) and vocal tract (Lieberman, 1968; Lieberman et al., 1969) involved in the production of particular vocalizations, mainly as an aid to understanding why humans have language while monkeys do not. All of the studies utilize the descriptive terminology established by Rowell and Hinde (1962) or earlier workers. To date, there has been no attempt to independently confirm with the aid of spectrographic analysis either the validity and exhaustiveness of the categories established or the invariant nature of the acoustic features which define each sound category. Considering the magnitude of research carried out on rhesus monkeys and the frequency with which this vocal descriptive terminology is used, such

independent investigation of the vocal repertoire would seem to be a useful precaution to prevent any pyramiding of error in the interpretation of experimental findings.

Vocal-Auditory Communication in Other Species of Macaca

As Andrew (1963) has pointed out, the vocal repertoires of congeneric species often contain sound signals which are species-specific. Additionally, apparently similar sounds can contain subtle differences which are processed by recipients in a species-specific manner (Zoloth et al., 1979). Despite these cautionary notes, the gross similarities in much of the vocal repertoires of the other species of macaque which have been studied to date requires some discussion. Features discovered in the vocal repertoires of other macaque species provide a useful basis for inquiring whether similar features may be found in the vocal-auditory communication system of the rhesus monkey.

Of the 12 species of *Macaca* defined by Napier and Napier (1967), the vocal repertoires of four species (in addition to the rhesus monkey) have been systematically examined. This includes the vocal repertoires of the Japanese monkey, *Macaca fuscata* (Itani, 1963; Green, 1972, 1975), the crab-eating macaque, *Macaca fasicularis* (a.k.a. *Macaca irus*) (Goustard, 1963), the pigtail macaque, *Macaca neminstrina* (Grimm, 1967), and the stumptail macaque, *Macaca arctoides* (a.k.a. *Macaca speciosa*) (Bertrand, 1969; Chevalier-Skolnikoff, 1974).

The behavior of feral Japanese macaque monkeys has been under scrutiny at the many feeding stations of the Japan Monkey Centre since the middle part of this century and vocal communication was among the first

aspects of social behavior to be studied. Although all of this early work is written in Japanese, Itani (1963) provides a comprehensive description in English of the vocal sounds used by the Takasakiyama group he studied. Itani noted 37 sounds which he classified into six major groups based on commonality of "social meaning or effect." Using letters and numbers as designators of the individual sounds, he gives extensive contextual information about each sound but his description of acoustic structure is limited since his work predates the use of spectrographic analysis. This represents a major shortcoming of his study although it should be noted that the degree of differentiation of sound signals which Itani achieved by ear alone is remarkable.

Green (1972, 1975) conducted a study of vocal communication in provisioned troops of Japanese monkeys at three localities in Japan. Using spectrographic analysis, he grouped sound signals into 10 classes based on the physical characteristics of the sounds and only later correlated these physically distinguished sounds with context (cf. Altmann 1962; Marler 1965). In an extended analysis of one class of sounds, the tonal "coo" sounds, Green showed how subtle structural differences (not easily distinguished by the human ear but discriminable on the spectrograms) could be correlated not only with different social contexts, but more consequentially, with differences in demeanor indicative of differences in underlying motivational state. He was able to conclude, therefore, that different kinds of coos may be used to communicate graded information about motivational state. One problem with this analysis, as Lillehei and Snowdon (1978) have pointed out, is that in sorting "coo" sounds by physical characteristics only, Green may have

inadvertently confounded physical characteristics of the sound which can be attributed to individualization of sounds (i.e., "vocal signatures"). This problem will be taken up again in Chapter IV.

While the preceding studies were carried out on free-ranging animals, four other studies have been conducted on captive animals. Goustard's (1963) study of *Macaca fascicularis* followed closely on the initial work of Rowell and Hinde (1962) and Andrew (1962, 1963) in the early use of spectrographic analysis for the structural analysis of sound signals used by a captive colony. In contrast to Rowell and Hinde's alternating attention to physical characteristics and function for constructing classification levels, Goustard paid special attention to function and discussed examples of sound signals used in specified contexts. This work is written in French and has not received much attention in the literature.

Much more frequent reference is made to a study by Grimm (1967) of the vocalizations of 35 captive pigtail monkeys which were individually caged in a laboratory. These animals were subjects in biomedical and learning experiments and their social and physical environment was the most restricted of any mentioned in this review. From a large data base of recorded sounds, 400 were spectrographically analyzed and then sorted without reference to situational context. The reliability of the sorting decisions was aurally checked by a panel listening to sample tapes. This study is notable for being the first to catalog macaque tonal sounds, of which 12 different kinds were noted. Additionally, 12 harsh and 5 high-pitched sounds were catalogued. Spectrograms of each of these sound signals were published but only limited information about associated behaviors is given.

The other macaque species whose vocal repertoire has been systematically examined is the stumptail macaque (Macaca arctoides) (a.k.a. Macaca speciosa). This repertoire was independently analyzed by Bertrand (1969) and Chevalier-Skolnikoff (1974).

Bertrand's study was initiated because very little was known about either the ecology or the behavior of a species which had begun to attract attention as a potentially superior subject for laboratory research because of its docility. Working with a series of captive stumptail groups at the Calcutta Zoo and the Paris Zoo (supplemented by a brief field study in Thailand), Bertrand's analysis of the vocal-auditory communication system of the stumptail macaque was part of a more general study of the major activity and communication patterns characteristic of this species. Basing her classification on physical characteristics, she catalogued and published representative spectrograms on 17 types of sound signals and described their behavioral context. She suggested that the total repertoire was probably larger than this and also emphasized that most of the sounds formed graded systems with intermediates existing between the labeled sound signals, a feature which Rowell and Hinde (1962) had earlier noted in the vocal repertoire of the rhesus monkey.

Chevalier-Skolnikoff (1974) observed a captive group of stumptail monkeys belonging to the Stanford University School of Medicine in order to determine how infant and adult communication differs and how the former matures into the latter. Although previous investigators had emphasized the primacy of visual communication (Rowell and Hinde, 1962), Chevalier-Skolnikoff was the first to quantify this. She found that 45 percent of the

communicative behavior of adult animals was visual, 41 percent was tactile and only 14 percent was vocal-auditory (p. 25). Her sound signal repertoire was much larger than Bertrand's, in part because she distinguished infant calls as distinctive vocalizations when they had counterparts in the adult repertoire. It is interesting to note, however, that Chevalier-Skolnikoff failed to find three of the vocalizations reported by Bertrand (Chevalier-Skolnikoff's data were collected before the publication of Bertrand's study) and she suggested that the vocal repertoire of stumptails may be even greater than the 28 sounds she distinguished. This latter finding emphasizes the usefulness of independent investigation of a single species.

The above studies make it possible to integrate the information derived by this investigator from the study of vocal behavior in the Silver Springs rhesus colony with a significant amount of published data on other species of macaque. As a result, one can begin to distinguish the more conservative from the more specialized features of the rhesus vocal-auditory communication system. Although it is somewhat surprising that a systematic comparison of vocal behavior across the genus Macaca has not yet been made, this deficit simply underscores the degree to which the analysis of primate sound signals is still in its infancy.

The Individualization of Sound Signals

In the history of ethology, Craig's (1908) analysis of the use of vocalizations "as a means of social control" in the pigeon is an early classic. Among the social functions he ascribed to pigeon vocalization was its use to "proclaim . . . the bird's individual identity." This early suggestion regarding

the importance of individual identification in the sound signals which animals emit to regulate social behavior had little effect on the next 50 years of research and theoretical development in ethology. Although a number of field observers had suggested that individual birds react differently to the same calls emitted by different individuals (and the field observers were themselves able to identify individual birds by ear), it was not until the 1960s that extensive analytic attention was directed to demonstrating individualization in sound signals. This included both an analysis of sound signals (aided by advances in instrumentation such as the sound spectrograph) to define the specific variable features of a call which might serve as cues to individual identity and an analysis of differential social responses to the same calls emitted by different individuals (for which the playback of recorded sound has been an especially useful technique).

Beer (1970) has provided a review of the earlier accumulated literature on individual recognition of "voice" in birds and the evidence which suggests how it may function in the maintenance of pair bonds, in territorial advertisement and defense, and in parent-offspring interactions. In recent years, further contributions to the ornithological literature on this subject have been made by Emlen (1971), Krebs (1971), White (1971), Goldman (1973), Brooks and Falls (1975a, 1975b), Harris and Lemon (1976), Berger and Lignon (1977), Wiley and Wiley (1977), Brooke (1978), and Mammen and Nowicki (1981).

The individualization of sound signals has received very little attention by mammalogists and primatologists. This relative neglect may be related to the fact that vocal communication does not occupy the salient position in the

behavioral repertoire of most mammalian species that it does among many bird species. Yet individual recognition (and individualized tailoring of social behavior) is an implied feature of some of the most basic concepts used in the analysis of mammalian social behavior including dominance, territoriality, xenophobia and kin selection. To the degree that any mammal uses sound signals to regulate social relations, it might be instructive to inquire whether individualization of signal form is a notable feature of these signals. To the degree that some mammalian species have evolved complexities of social regulation which surpass anything found in the bird species studied to date, it may be possible to define new and subtle subsidiary functions for any individualization of sound signal which is discovered.

There has been, within the last two decades, a virtual explosion in the accumulation of data about the social behavior of non-human primates. It is not surprising, therefore, that most investigations of individuality of vocalizations have been conducted on member species of this order. Of the non-primate mammals, only dolphins (Caldwell and Caldwell, 1965), elephant seals (Petrinovich, 1974), and reindeer (Espmark, 1971, 1975) have been investigated for evidence of individual recognition of voice and/or individualization of sound signals. Among non-human primates, pigtail macaques (Simons et al., 1968), rhesus monkeys (Hansen, 1976), grey cheeked mangabeys (Waser, 1977), squirrel monkeys (Kaplan et al., 1978), vervets (Cheney and Seyfarth, 1980), and pygmy marmosets (Snowdon and Cleveland, 1980) have shown evidence of individualized responses to playback or spontaneous emission of the calls of significant conspecifics. Reliable individual differences in the structure of particular sound signals (individualization which can provide a

basis for individual recognition) has been shown in chimpanzees (Marler and Hobbett, 1975), stumptail macaques (Lillehei and Snowdon, 1978), and pygmy marmosets (Snowdon and Cleveland, 1980).

Much of the work on individualization of sound signals in mammals has focused on the recognition of mother-offspring pair members for each other (Simons et al., 1968; Espmark, 1971; Petrinovich, 1974; Hansen, 1976; Kaplan et al., 1978; Cheney and Seyfarth, 1980). In addition to these experimental investigations, incidental observations on apparent mother-offspring recognition by voice have been reported and these are summarized by Spencer-Booth (1970). While it is not difficult to argue for the adaptive value of mother-offspring recognition by voice, other possible functions of voice recognition have received little attention. Only Waser (1977) has experimentally investigated how individual recognition by voice may function in the intra-group cohesion and intergroup spacing of feral mangabeys.

Since vocalizations show evidence of being conveyers of categorical information, the accumulating evidence for individualization of sound signals produces an apparent conflict of selection pressures. One might argue that selection should have favored the evolution of stereotyped, invariant features for particular calls in order to reduce ambiguity and increase signal clarity (cf. Morris, 1957). Selection for individualization of sound signals increases variability and might be said to increase ambiguity. Snowdon (1979) and Snowdon and Cleveland (1980) have dealt with this problem by suggesting that sound signal recognition may function in a two-stage manner. In the first stage, an animal classifies an incoming call into a broad category using either invariant features or features which do not vary beyond certain sharp

boundaries. In the second stage (which may be either simultaneous or subsequent), the animal "makes use of the variability within the signal to extract additional information" (1980, p. 726) including information about the identity of the caller. In this way, both selection for signal clarity and selection for individualization ("both categorization and within-category discrimination of sounds" (1979, p. 427)) can occur simultaneously.

With the above considerations in mind, it is now possible to turn to an analysis of vocal-auditory communication among the rhesus monkeys of Silver Springs to examine the evidence for both categorization and individualization of sound signals.

CHAPTER II

THE SILVER SPRINGS RHESUS COLONY

The Physical and Human Setting

Silver Springs is a limestone artesian spring formation whose large water outflow (averaging 820 cubic feet per second) produces the five-mile long Silver River, a major tributary to the Oklawaha River (Rosenau et al., 1977). The clarity, depth and volume of the water flowing out of the major boils and the subtropical vegetation lining the banks of the river have made this site a commercial tourist attraction since the second half of the 19th century. It became especially famous as the first site to use glass bottomed boats for viewing the underwater scenery. Since 1962, the commercial area around the mainsprings has been managed by the Leisure Attractions Division of the American Broadcasting Companies, Inc. This corporation also owns 3,900 acres of undeveloped land immediately adjacent to the Silver River (Martin, 1966). Silver Springs has been designated an Historic National Landmark by the National Park Service of the U.S. Department of the Interior.

Located in Marion County at 29°N latitude and 82°W longitude (6 miles northeast of the city of Ocala), Silver Springs has a mild climate. During 1978, average daily temperature for Marion County ranged from a low of

50.6°F (10.3°C) during February to a high of 80.8°F (27.1°C) for August. The highest recorded temperature was 98°F (36.7°C) on August 29, 1978, and the lowest recorded temperature was 20°F (-6.7°C) on January 16, 1978. The annual rainfall was 49.35 inches (125.3 cm.), with nearly 22 inches (55.9 cm.) falling during the summer months of June, July and August (NOAA, 1978). The average frost-free season has been calculated for nearby Gainesville to be 295 days (Dohrenwend, 1978).

Silver Springs lies in the transition zone between a subtropical Caribbean flora and a warm temperate flora and the vegetation reflects some of the characteristics of both (Dohrenwend and Harris, n.d.). The results of a survey (commissioned by the America Broadcasting Company and carried out by the engineering firm of Reynolds, Smith and Hills of Jacksonville, Florida) are graphically presented in Figure 1. The floodplain immediately adjacent to the Silver River, where the monkeys are most frequently observed, is described in their report as an area dominated by tupelo gum (*Nyssa biflora*), bald cypress (*Taxodium distichum*), sweet gum (*Liquidambar styraciflua*), red maple (*Acer rubrum*), and red bay (*Persea borbonia*). The understory consists of Virginia willow (*Itea virginica*), bracken fern (*Pteridium aquilinum*), and cinnamon fern (*Osmunda cinnamomea*) [Reynolds, Smith and Hills, 1977, p. 10]. Figure 2 illustrates the floodplain community in summer foliage.

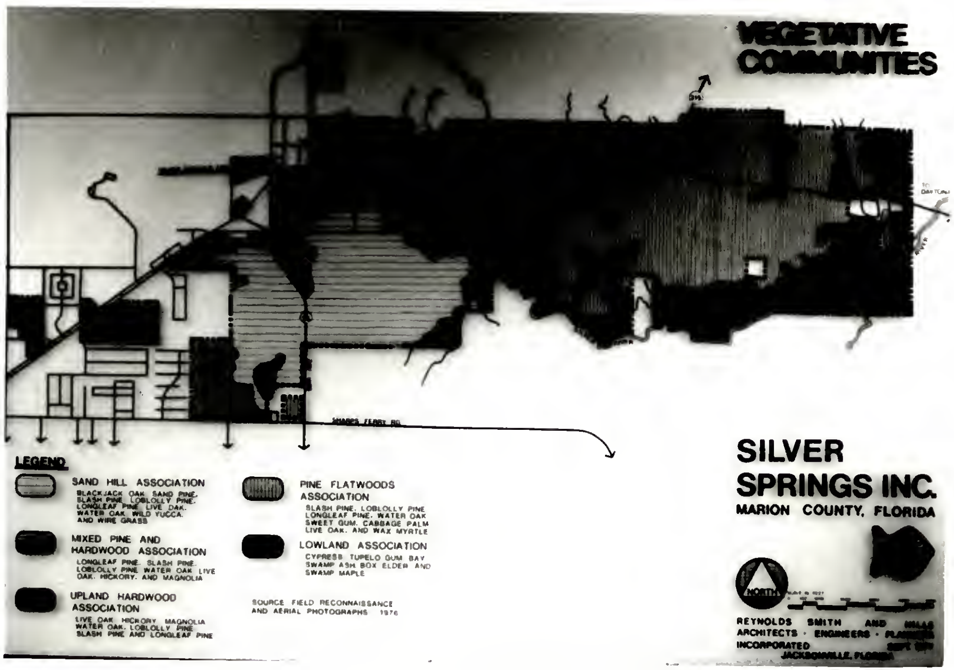

Figure 1 Vegetative communities of Silver Springs.

Figure 2 Lowland association community adjacent to the Silver River.

Inland and upland, from the river floodplain, lies a community through which the monkeys occasionally traveled, described by Reynolds, Smith and Hills as "Sand Hill Association." The major tree species in this zone are blackjack oak (Quercus leavis), sand pine (Pinus clausa), loblolly pine (Pinus taeda), and longleaf pine (Pinus palustris), with an understory consisting mainly of myrtle oak (Quercus myrtifolia), wire grass (Aristida stricta), prickly pear cactus (Opuntia), and several types of ground growing lichens (Cladonia) [Reynolds, Smith and Hills, 1977, p. 111]. Both of these communities show evidence of human disturbance including trails and the results of logging activity.

Systematic surveys of the fauna in these communities have not been undertaken but a few general observations can be stated. Of the larger mammals, only whitetail deer (Odocoileus virginianus), raccoons (Procyon lotor), nine-banded armadillos (Dasypus novemcinctus), river otters (Lutra canadensis), oppossums (Didelphis virginiana) and feral domestic hogs have been sighted by this investigator, mostly in the floodplain near the river (since this is where most observation time was spent). Also reported to be in this area are the bobcat (Lynx rufus), the gray fox (Urocyon cinereoargenteus), the marsh rabbit (Sylvilagus palustris), the panther (Felis concolor) and perhaps the black bear (Ursus americanus). Gray squirrels (Sciurus carolinensis) are commonly observed during the day, while unidentified species of small rodents (Cricetinae and/or Murinae) have been observed near the monkey's provisioning area in the evening and unidentified species of bats (Chiroptera) navigate the river at night.

Martin lists 29 species of birds commonly seen around Silver Springs (1966, pp. 208-211). Most of these are found on the river or near the river's edge, although the pileated woodpecker (Dryocopus pileatus) and the cardinal (Cardinalis cardinalis) have also been sighted inland. Of the raptorial species, turkey vultures (Cathartes aura) and red-shouldered hawks (Buteo lineatus) have been sighted soaring over the river and adjacent floodplain, while osprey (Pandion haliaetus) are reported to be in the area.

Of the reptilia, the American alligator (Alligator mississippienisis) is a dominant feature of the river landscape. Several species of turtles live in or near the river, although only the box turtle (Terrapene carolina) can be observed in the floodplain area with any appreciable frequency. Snakes are occasionally sighted, including the eastern diamondback rattlesnake (Crotalus adamanteus). Small lizards are plentiful, particularly anoles (Anolis carolinensis).

Of the many species of insects and related invertebrates which populate this area, two are particularly noteworthy as a nuisance to monkeys and humans. These are the American dog tick (Dermacentor variabilis) and the chigger (the larvae of mites belonging to the family Trombiculidae). Mosquitoes attack humans, but do not seem to be troublesome to monkeys.

The monkeys' use of this habitat for subsistence has been reported in Sarris (1980) and will not be repeated here. Interaction with the major fauna species was limited. On a few occasions, small lizards, a turtle and a raccoon became objects of playful attention by juvenile monkeys. Raccoons, deer and feral hogs were occasionally seen at the provisioning site and competed with the monkeys for the available food. While deer and hogs passively displaced

the monkeys at this site, raccoons were in turn displaced by the monkeys who sometimes threatened vocally and chased the raccoons away from the food. The sight of an alligator approaching the riverbank always elicited warning calls from one or more monkeys and respondent flight into the trees. I never observed predation by an alligator on a monkey, but I did collect one report of such an event from one of the maintenance personnel.

History of the Silver Springs Monkey Colony and Its Scientific Investigation

The most frequently repeated anecdote regarding the origin of the Silver Springs rhesus colony is that the present population is descended from a small number of animals which were released for the filming of one or more Tarzan movies sometime during the 1930s. Since 1929, when the first sound movie was filmed at this site, Silver Springs has been a popular location for commercial movie-making. Martin (1966, p. 161) states that six Tarzan movies were produced by MGM at this time, although Anthony Slide, the coordinator of the National Film Information Service, was only able to locate records relating to one Tarzan movie. This was "Tarzan Finds a Son," released by MGM in 1939 (Slide, personal communication).

Sometime after their initial release, the human interest value of monkeys along the banks of the Silver River began to be exploited by tourboat operators. In addition to regular feeding by tourboat drivers, rumors persist that there may have been subsequent releases of monkeys to ensure the survival of the colony. Since the monkeys have never been trapped and blood tested, the degree of genetic homogeneity in this colony is unknown.

The first scientific investigation of rhesus presence along the Silver River was conducted in 1971 by William R. Maples of the University of Florida and his student Michael Hutchins [Maples, 1976]. By this time, the commercial boat tours were managed by the American Broadcasting Company, the monkeys received regular provisions and the colony seemed well established. Two feeding sites (one on each side of the river) had been established about 3/4 of a mile below the headsprings and the monkeys had become accustomed to receiving food at these locations. A 1968 census had indicated a total of about 78 monkeys divided among a north bank and a south bank troop (Maples et al. 1976).

In 1973, Judith Breuggeman, then a student at Northwestern University, censused the Silver Springs monkeys in January and July. From September to December 1973, she spent approximately 210 hours tracking the onset and advance of the mating season in this colony, noting that it seems to lag several months behind the mating season in the comparable rhesus monkey colonies located on Caya Santiago and La Parguera, near Puerto Rico. In 1976, Breuggeman again spent one week censusing monkeys (Breuggeman, personal communication).

In January 1976, William R. Maples, then an associate curator with the Florida State Museum, began a long-term study (via boat and on land) of a single group of about 26 monkeys located on the southside of the river. He was successively assisted by Antoinette B. Brown, then an assistant professor at the University of Florida, and several students, including myself. During this period, all of the adult animals in this group were identified and named. A record of changes in group composition was initiated which continues

through the present. Among other observations, Maples was able to document a split in the southside group which occurred when the main group of monkeys left the provisioning area for an extended period of time (June to December 1976), while a small remnant group of seven monkeys stayed behind. Upon their return to the provisioning area in December 1976, the wandering southside monkey group no longer affiliated with the remnant group and relations between the two became agonistic (Maples, personal communication and author's personal observations).

Beginning in August 1977, this investigator assumed primary responsibility for maintaining regular observations on the main southside group. From August 1977 through March 1978, all observations were made from a private boat, but in April 1978, land-based observation was initiated and this proved much more productive for the collection of data. In addition to collecting general information about foraging habits (Sarris, 1980), troop movements and social behavior, I began in April 1978 to investigate in detail the use of vocal communication in this monkey group. This investigation continued through May 1979 and included approximately 770 contact hours with the monkeys.

In September 1980, Linda D. Wolfe, a visiting assistant professor at the University of Florida, initiated land-based observations on the reproductive behavior of the southside rhesus group and her work is now continuing. Preliminary results were presented at a recent meeting of the Florida Academy of Sciences (Wolfe et al., 1981) and in a report to the Leisure Attractions Division of the American Broadcasting Companies, Inc. [Wolfe and Peters, 1981].

In an attempt to learn more about the number, size and distribution of monkey groups located north of the Silver River, this investigator organized in March, 1981, a survey of these animals with the help of John G. Robinson (director of the Third World Biology Training Program located at the Florida State Museum), Linda D. Wolfe and students from the University of Florida. Two large troops (each in excess of 50 animals) and several solitary males were seen by the teams, indicating that there seem to be at least 100 monkeys inhabiting the floodplain area just north of the river [Peters et al., 1981]. Combining these estimates for the north bank troops with the numbers of known animals occupying the south bank suggests a total population of at least 170 monkeys in this colony as of spring 1981. This is a conservative estimate and the actual number is probably larger.

Social Group Dynamics

As is true for any free-ranging social animal, the composition of the southside rhesus group has been in yearly flux due to the unending cycle of births, deaths, emigrations, immigrations, and group splitting. Table 1 summarizes the composition of this study group during the period 1976-1981. The sharp drop in group size from 1976 to 1977 was due to the group split described earlier, while the steady increase in group size from 1977 to 1981 was primarily due to a birth rate in which an average of 75 percent of the pubescent and adult females in the group gave birth to surviving offspring each year. With one exception (discussed below), all of the immigrants into the group between 1977 and 1981 and all missing monkeys (emigrants or deaths) were male.

Table 1. Age-Sex Composition of the Southside Rhesus Group 1976-1981[1]

	[3]1976		1977		1978		1979		1980		1981	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Adults[2]	9	6	4	3	6	3	8	3	10	2	11	2
Subadults[2,3]	-	-	2	1	1	3	2	5	1	4	2	6
Juveniles[2]	5	5	3	6	5	5	4	7	7	8	21	
Infants[2,4]	2	4	2	1	1	3	4	4	9		10	
Total by Sex	16	15	11	11	13	14	18	19				
Group Total	31		22		27		37		41		52	

1. These counts include all monkeys in the troop after the spring birth season (and therefore include all new infants) but before the emigrations and immigrations characteristic of the mating season.

2. Adult = 7 years + for males; = 5 years + for females. Juveniles = 1-3 years

   Subadult = 4-6 years for males; = 4 years for females. Infants = less than 1 year

3. Information about group composition in 1976 was provided by W.R. Maples. Maples does not distinguish a subadult category in his age classification. All animals over fours years of age were considered to be adult animals.

4. During 1980 and 1981, not all infants were sexed and I am not able to give a breakdown by sex for infants or the entire group for these years.

During the fall of 1978, the southside group consisted of seven adult females (aged 5 years or older), 3 adult males (aged 7 years or older), one subadult female (aged 4 years), 10 juveniles (1 to 3 years old), and 4 infants (less than one year). From April through July 1979, 8 new infants were born into the troop. A semi-independent subgroup consisting of four subadult males (4 to 6 years of age) was usually seen peripheral to the main study group during fall 1978 and winter-spring 1979. All but one of the males had never been observed by this investigator before October 1978 and all were probably non-natal males. The three adult males and four subadult peripheral males could be arranged in a dominance hierarchy which remained stable from October 1978 through May 1979. Table 2 summarizes their rank order and also serves as an introduction to these animals.

As identification of individual animals became reliable, mother-focal subunits became apparent which included persistent patterns of proximity, allogrooming and mutual defense. The genealogical chart shown in Figure 3 summarizes these important biosocial bonds and and also serves as an introduction to the females and their offspring. The females who had associated offspring in 1977 are listed in order of decreasing age. Ages for monkeys born before 1976 are estimates which become increasingly rough for animals born before 1973. Males born to the troop before 1975 are not shown since all had left the troop by fall 1978 and their maternal affiliations were never clear. Four females (LS, KA, CL, DO) who were subadult or juvenile in 1977 when I began my studies could not be confidentally affiliated with any of the older females. The affiliation tendencies of their own offspring led me

Table 2. Adult and subadult males in the southside group from October 1978 to May 1979, arranged by dominance rank.

	Rank	Name of Male	Estimated Year of Birth
Adult Males	1	DM	pre-1969
	2	LR	1970 or 1971
	3	CS	1970 or 1971
Subadult Males	4	JR	1972
	5	WL	1973
	6	HV	1974
	7	JM	1974

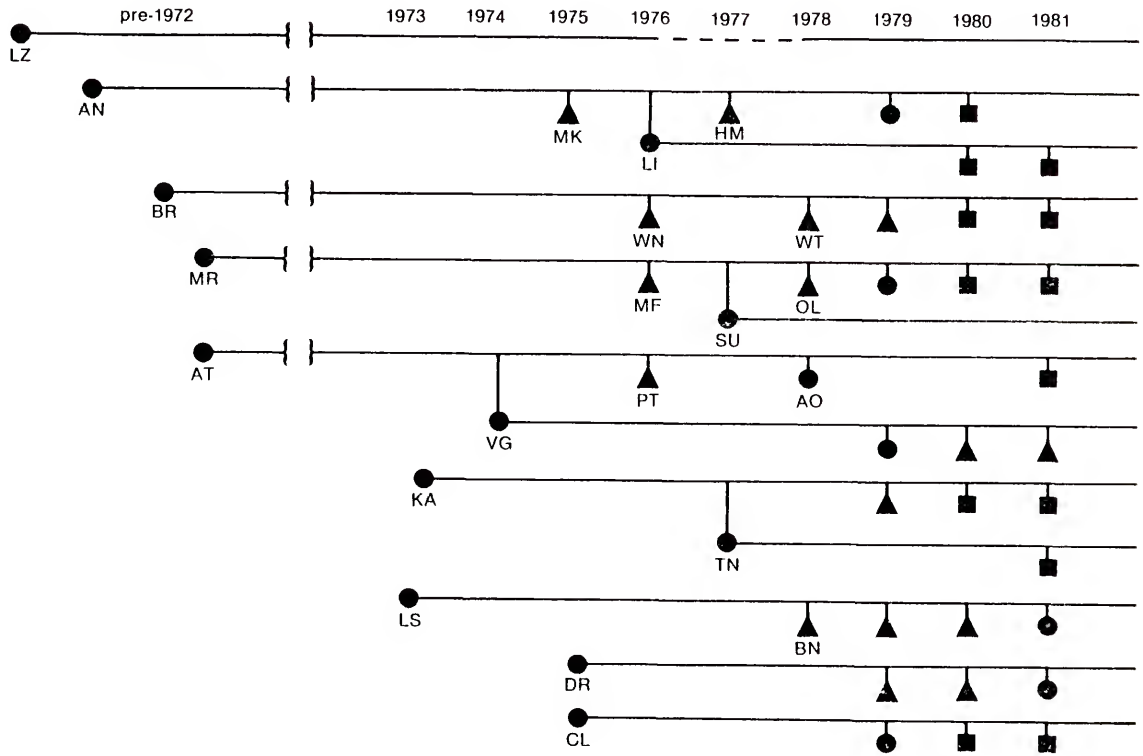

Figure 3. Females in the southside group from 1977 to 1981 and their associated offspring. ● = females; ▲ = males; ■ = animals of unknown sex.

to suspect that LS may be the daughter of AN, while KA may be the daughter of BA. CL and/or DO may be the offspring of females now in the remnant group which split off in 1976.

One old female (LZ) was never seen with dependent offspring and has been sterile (although sexually active) since at least 1976 when regular observations were begun on this group. After the 1976 group split, she was not observed in regular association with either the main southside group or the remnant group, but during the mating season of 1978 she reintegrated with the southside group. From her labored gait, baggy skin and post-reproductive status, I surmised she was probably 20 years or older in 1977.

The last social element of which some mention should be made are the solitary males. These were sighted on the periphery of the main study group with greatest frequency during the mating season (from November 1978 to January 1979). They were always fully adult animals and although they never vocalized, their jumping displays in high trees were often effective in drawing the attention of females who were later seen in consort with them.

Activity Patterns and Ranging Behavior

As diurnal animals, the major activity patterns of the southside rhesus group were geared to the light cycle. The monkeys slept in trees, usually in small family clusters. They did not seem to have regular sleeping sites (cf. Lindburg 1971; Makwana, 1978); rather as darkness approached, more and more of the animals could be observed in the trees wherever the group happened to be. Finally, over a long period of increasing darkness, all animals settled into relatively stable sleeping clusters. Usually the group did not move at night, but I did note occasions when the group seemed to be

asleep for several hours, then became aroused and moved through the trees. Often this was in response to the appearance of one or more strange monkeys in the vicinity.

At daybreak, the juveniles were often the first and the adult animals were often the last to descend from the trees. During the period of my observation, the monkeys received provisions (including monkey chow and fresh fruits and vegetables) at 8:30 a.m. and 4:30 p.m. When the monkeys were in the vicinity of the provisioning site, the entire group became very vocal and approached the feeding site in response to the sound of the maintenance boat (which delivered the food) traveling down the canal.

The morning feeding was often followed by a period of relative inactivity or relaxed social grooming. During the warmer months, the animals stayed on or near the ground, but in the colder, winter months, they often ascended to sunny spots in high trees to doze and groom. During the middle part of the day, at least some animals oriented to the calls of tour boat drivers and returned to the provisioning site to receive bread, fruit or peanuts. This cycle might continue throughout the day, interspersed with periods of foraging, grooming, exploring, resting, playing, or intragroup aggression and defense. The monkeys might maintain a relative proximity to the provisioning site throughout the day (particularly during the colder, winter months) or they might at any time of the day start moving downriver, a journey from which they usually did not return to the provisioning site the same day.

The ranging and foraging behavior of the southside rhesus group does not seem to be explainable in terms of food stress (Sarris, 1980). While it was

not the focus of my study, a few preliminary observations on this behavior can be stated. In most of their ranging, the study group confined themselves to within 200 meters of the river and therefore stayed in the lowland, floodplain area. The maximum distance I followed them down river was 2 1/2 km., but this was because the monkeys crossed to the north bank of the Silver River and it was no longer possible for me to follow them. Although most of this ranging was short term and the monkeys returned to the provisioning area within one or two days, there were at least two occasions when the group was not sighted at the provisioning area for many months (June to December 1976 and July to October 1978). The tendency of rhesus monkeys to sometimes move outside of their normal range has also been noted by Neville for forest-dwelling animals near Haldwani in Uttar Pradesh (1966, p. 117).

Data Collection and Analysis

Behavior sampling in the field was a combination of *ad libitum* and sequence sampling (Altmann, 1974). Focal animal sampling was not undertaken because heavy underbrush in some parts of the study area made visibility poor and preliminary attempts to maintain prolonged contact with a single moving animal had proved to be very disturbing to the behavior of both the subject animal and other group members. These animals were (and continue to be) only marginally habituated to land-based observation, despite their frequent exposure to humans in boats.

During periods of silence, I *ad libitum* sampled the behavior of conveniently visible animals with a general attempt to distribute my observation time so that over the week most animals were observed. In addition to

focusing on the behavior of one animal or a small group of animals, I also attempted to maintain a general awareness of the nature of the total social field. Notes taken during these sampling periods were spoken into a cassette recorder and later transcribed. Cassette notes have the advantage of allowing unbroken visual contact with the animals and detailed information can be recorded in a short period of time. The disadvantage is that access to these notes is not immediately available and transcription is relatively time consuming.

The vocalizations of the monkeys were recorded with a Nagra III open reel recorder operated at 7.5 inches per second and a Sennheiser directional condenser microphone composed of a K-3U module and an ME-80 head. This recorder was activated and I began sequence sampling whenever one or more animals vocalized. While recording the vocalization(s) on the Nagra, I made separate spoken notes on the cassette recorder, including all notable behavior preceding, during and immediately after the vocal event. This included the behavior of the vocalizing animal(s) and all responses by other animals which were apparent to me. Whenever possible, the identity of the vocalizer(s) and the respondent(s) were noted. Notes on the cassette recorder were calibrated by time entries to vocal events on the Nagra.

Spectrograms of the monkey vocalizations were made on a Kay Sonagraph 6061A using a 150-Hz filter to scan the 80-8,000 Hz range. This filter was chosen because it gave good harmonic separation while minimally distorting the temporal dimension.

In order to provide reliable access to individual vocalizations, an index to the Nagra tapes was constructed by listening to the tapes on a TEAC

A-7300 tape recorder which is equipped with a timer. Individual sounds were assigned an entry time which could then be cross-referenced to the number assigned to each spectrogram that was made.

CHAPTER III

A CATALOGUE OF RHESUS VOCALIZATIONS

Rhesus vocalizations, as any investigator who has worked with these animals will attest, exist in almost bewildering variety. Finding the organizing patterns in this sound system is no small task as Altmann (1962), Rowell and Hinde (1962), Lindburg (1971), and Erwin (1975) have pointed out.

The usual approach to the analysis of animal vocal repertoire is to define a series of relatively stereotyped, distinct acoustic units (the "vocalization" or "call") each with its own meaning or message. The message, although not always easy to ascertain, is inferred from an analysis of the stimulus situation, the behavioral probabilities associated with the vocalizing animal(s), and the response probabilities associated with the recipient(s) of the signal. There are two major problems with this approach, both of which reflect the difficulty of defining that basic unit we call the "vocalization" or "call."

The first problem which greets the would-be taxonomer of rhesus sound signals is the realization that the rhesus vocal communication system does not exist as a series of relatively equal-sized units which can be called up as needed. Rather, as Jolly has pointed out in the context of a general discussion of communication units, "almost any unit that one chooses has subcomponents that vary somewhat independently, and in turn is itself a

component of larger units, in which it will contribute to different meanings" (1972, p. 146). When should an emitted sound be considered a complete "vocalization" and when should it be considered a subset or component of a "vocalization"?

Related to this problem of levels, there is the co-existing problem of defining the physical boundaries of the vocalization. Some of the sounds which monkeys and other animals emit reproduce spectrographically as fairly continuous tracings separated by intervals of several seconds (or more) from other such continuous tracings. However, other sounds reproduce spectrographically as a time-compressed series of similar-looking units and still others reproduce as a series of dissimilar-looking units. How much of the picture should be considered a single "vocalization"?

Robinson (personal communication) has suggested that a vocalization can be defined as the sound produced by an animal during a single inhalation-exhalation sequence. Aside from the difficulty of reliably discriminating when the animals is drawing a new breath, this definition may give too much status to sounds which never function in isolation as independent units.

In the following catalog of rhesus sound signals, an attempt will be made to define a "vocalization" as a functional unit. Thus, any sequence of sound which normally and frequently functions as a whole unit will be considered a vocalization. By this definition, each of several levels of sound (both wholes and parts) will be called a "vocalization" if they frequently function as independent units. However, components which are rarely or never emitted in isolation will not be given the status of "vocalization" regardless of the audible and spectrographic distinctiveness of the

component. Not audible distinctiveness but evidence of functional independence becomes the defining criterion of an individual "vocalization" or "call." (To suggest that a train of sounds "functions" as a single entity is to suggest that the whole was selected for and it is useful for researchers to examine the entire entity as cause and as effect in order to determine its meaning.)

There is a second major problem which confronts the taxonomer of sound signals, that quality of the rhesus communication system which is usually referred to as "grading." In order to clarify both the meaning of this term and why the phenomenon represents something of a problem for standard classification procedure, it is useful to introduce certain ideas and concepts which have been applied to communicative behavior by ethologists.

Communication has been broadly defined by Mason and Hollis (1962) (following Newcomb, 1953) as "any observable behavior by which information is transmitted from a social source to a social recipient (p. 211)." Using this definition, motor acts and autonomic responses which evolved for other purposes but which <u>incidentally</u> result in a transfer of information can be called communication. However, when these same motor acts or autonomic responses come under selective pressure to make the <u>communication</u> more effective (i.e., less ambiguous, of unmistakable meaning) than <u>a more evolved form of communicative behavior</u> makes its appearance. The process by which an otherwise useful behavior is transformed by selection into a less ambiguous signal is known as "ritualization" and the end-product is known as a "display" (Huxley, 1914). As Jolly (1972) has pointed out (following Morris, 1957), signal clarity and lack of ambiguity are enhanced when an act is

exaggerated, stereotyped and repeated and these features are the hallmarks of "displays" (1972: 145).

Although the term "display" has not been widely used with reference to sound signals (but see Moynihan 1956; Smith 1977), many of the vocalizations produced by non-human primates seem to fit the definition. They are distinctive and stereotyped in physical form, and they seem to be the end-products of selection for unambiguous transfer of specific information. However, some primate vocalizations are not so stereotyped in form. The vocal repertoires of rhesus monkeys and chimpanzees (to take two well-known examples) seem to include a large range of sounds not just a few types. Many of these sounds are referred to as "intermediates" or "variants," but these terms still imply that structured calls can be defined with "intermediates" existing between the types or "variants" existing as departures from the type. This typological conceptualization needs to be critically examined. While it may at times be useful, it is not necessarily the only, or always the best, way to understand what is going on.

An alternate way of conceptualizing primate calls is to see how some calls can vary almost continuously along gradients of intensity, pitch, duration, cadence, etc. and to see how each individual call can be the <u>unique</u> blend of an independent position along these several gradients simultaneously. The study of primate vocalizations then becomes a search for the meaning of change along each gradient rather than a search for the meaning of a limited number of call types. For many calls there may be some typical position along one or more of the gradients and when there is a typical position along all the gradients, a stereotyped sound signal is the result. For other calls,

there may be a great deal of variability along several or even all of the gradients and in this event it becomes exceedingly difficult to define a limited number of calls.

In the following catalog both the stereotypy of some rhesus sound signals and the lack of stereotypy in others will be noted. Since categorization into a limited number of calls is a convenience for human observers, an attempt will be made to define such a limited number. We should bear in mind, however, that in many cases we are defining a convenient fiction and not an absolute type.

There are several ways of cataloging sound signals. These include sorting sounds by physical structure (Green, 1975), by stimulus situation (Struhsaker, 1967), by dominant emotional tone and social context (Itani, 1963), or by a combination of the above factors (Rowell and Hinde, 1962; Grimm, 1967). In the following catalog, physical structure, dominant emotional-motivational message, and social context have all been considered. Wilson once suggested that " . . . if the construction of categories is hopeless, it is also profitable. Loose classifications, when not taken too seriously, can provide new insights into old phenomena and they can suggest new avenues for future research" (1975, p. 217). It is in this spirit that the following catalog is offered.

Definition of Terms

Rhesus vocalizations can be sorted on the basis of physical structure into those which are exclusively atonal, those which are predominantly tonal and those which include a combination of both atonal and tonal sound. Atonal

calls contain energy distributed relatively continuously over a wide range of frequencies and have also been referred to as "harsh noises" (Rowell and Hinde, 1962), "noise" (Andrew, 1963), "harsh sounds" (Grimm, 1967) and "nontonal units" (Struhsaker, 1967). Tonal calls contain energy concentrated in one or more narrow frequency bands and have also been referred to as "clear calls" (Rowell and Hinde, 1972), "sound" (Andrew, 1963), "harmonic sounds" (Grimm, 1967), and "tonal units" (Struhsaker, 1967). The term unit will be used, as defined by Struhsaker (1967), to refer to "a continuous tracing along the temporal (horizontal) axis of the sonogram" (p. 282). The term call or vocalization will be used, as defined earlier, to refer to any sequence of sound which can function as an independent whole. Unless othewise noted, every call is described on the basis of spectrograms derived from at least three different animals so that trans-individual features of the call provide the basis of the description. To avoid introducing unnecessary new terminology and to aid comparability with previously published catalogs, descriptive terms provided by earlier workers will be used whenever possible.

Atonal Calls

Certain calls which are completely atonal in structure are used in conjunction with behaviors which suggest that the calls impart a threat message. Recipients of this message tend to respond with rapid retreat from the caller or with counterthreat. Charges (and countercharges) may accompany the calling. Other completely atonal calls are used in conjunction with behaviors which suggest that they are imparting a message which can best be described as devoid of threat, fear or other aversive emotional-motivational

states. Recipients of this message are unlikely to retreat, and will either maintain their position or (in the case of one atonal call) will approach the caller and begin grooming him/her. Calls which are predominately atonal but which contain hints of harmonic structure and are consistently high in pitch are used in conjunction with behaviors suggesting that they impart a distress or fear message. This message may provoke attack by third parties toward an alleged "aggressor" or they may stimulate rapid flight into the safety of the trees by all monkeys in the immediate vicinity. Each of these three general message categories will be examined separately.

It should be noted that the term "threat message" need not imply that the initiating motivation of the vocalizing monkey is rage. A subordinate and easily frightened monkey who sat calmly in my vicinity for long periods of time might suddenly begin to threaten in my direction when a more dominant monkey approached us. The subordinate monkey would return to calm sitting after the dominant animal passed. Such an animal may be experiencing fear (of the approaching conspecific), but the message conveyed in the vocal signal is threat (directed toward the human observer).

Threat Calls

Rhesus monkeys produce a variety of threat calls. The broken (staccato) quality of many of these calls was first noted by Chance (1956) who used the descriptive term "hough-hough" to refer to all of these calls. Altmann (1962) similarly lumped all threat vocalizations under the onomatopoetic term " !Ho! " (behavior pattern #29 in his catalogue). Rowell and Hinde (1962), using spectrographic analysis, distinguished four kinds of atonal threat calls and labeled these respectively the "bark," the "pant threat," the

"roar" and the "growl." Since the Rowell and Hinde catalog has, as Erwin (1975) pointed out, "become the standard system for describing rhesus vocalizations," this terminology is now in wide use.

This investigator believes that the earlier workers may have had a more useful conceptual framework when they lumped all threat sounds into a single category and that the new terminology introduced by Rowell and Hinde may have created certain conceptual blinders for later workers (although Rowell and Hinde were themselves flexible in their thinking). I would like to suggest that all of the threat sounds produced by rhesus monkeys can be generated by the independent manipulation of five gradients.

1) a number of units gradient
2) a length of unit(s) gradient
3) a cadence gradient
4) an intensity (volume) gradient
5) a pulsation or trilling (vertical striation) gradient.

In order to illustrate how these gradients operate, I will arbitrarily distinguish three types of threat calls based on the number of units. These will be called <u>one-unit pant threat</u>, <u>two-unit pant threat</u>, and <u>multi-unit pant threat</u>.

Before presenting these three call types, it might be useful to present the features which various sounds have in common. In terms of acoustic morphology, two characteristics stand out. First, the constituent unit sounds are neither very long nor very short when compared to the constituent units of other calls in the rhesus repertoire. They average about 250 milliseconds in length. When given in series, the units are spaced about 200 milliseconds apart. Second, the energy tends to be relatively evenly distributed along the

frequency axis with no very obvious concentration of energy at a particular and consistent frequency (or frequencies).

In terms of behavioral correlates, all threat calls are produced with the lips in a protruding position (see Figure 4) and are always accompanied by visual signals. At low intensity, the visual signal may be a simple stare at the intended recipient while the body remains relatively relaxed; at higher intensity the visual signal may involve the whole body in a postural display (Figure 4), or the sound may even accompany a full physical attack. Most threats, particularly the multi-unit vocal threats, seem to have a rallying effect on other members of the group and a large number of monkeys may be motivated to join in an attack initiated by a single monkey. Vocal threats also provide an animal an opportunity to participate in an agonistic encounter while remaining at some distance from it and/or may rally full physical participation over a wide area.

One-unit pant threats

Figures 5 and 6 illustrate two examples of a one-unit pant threat given in a similar stimulus situation. In each case, a short (less than 250 milliseconds) noisy sound with energy distributed over a wide frequency range is accompanied by a simple stare. Figure 5 is undoubtedly identical to the call which Rowell and Hinde called a "bark," while Figure 6 is the call which they labeled a "growl." A "growl" differs from a "bark" in having the sound broken up along the horizontal axis into a series of vertical striations which make the call sound trilled. Rowell and Hinde suggest that the "growl" is quieter (less intense) than the "bark," but I have noted trilled calls which can be more intense (louder) than some untrilled threat calls. Whether there

Figure 4 Subadult male emitting a multi-unit pant threat.

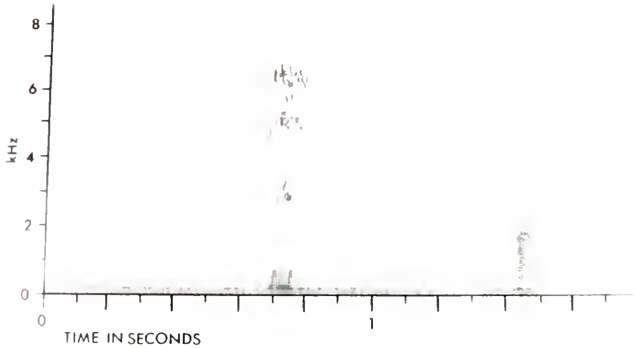

Figure 5 Spectrogram of one-unit untrilled pant threat.

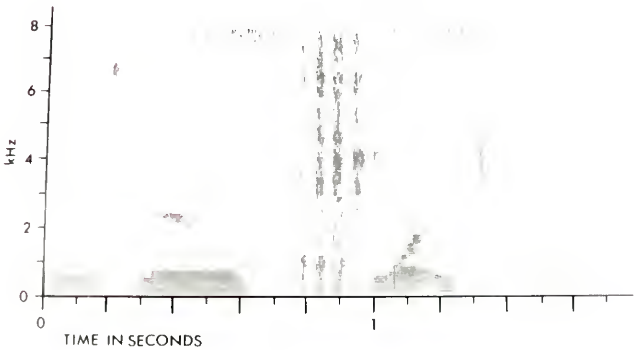

Figure 6 Spectrogram of one-unit, trilled pant threat.

is some necessary correlation between intensity and trilling is yet to be determined. Rowell and Hinde did note that "intermediates" between the "bark" and the "growl" occur "in all gradations" and Figure 7 is an example of a sound emitted in a threat context which shows only a limited amount of trilling.

Two-unit and multi-unit pant threats

Rowell and Hinde did not chose to distinguish two-part threat sounds as separate calls, but I have frequently noted two-unit threat calls such as those illustrated in Figures 8 and 9. Note that two-unit threat calls may be trilled (Figure 9) or untrilled (Figure 8) suggesting that trilling is a gradient which may be varied independently of number of units. In two-unit pant threats, there is often an unequal intensity emphasis among the units (usually the second unit is more intense) and it is possible that the first unit of noise may be an inspiration sound.

Figure 10 shows a part of a multi-unit pant threat in which no vertical striation is evident and Figure 11 shows three units of a multi-unit sound in which trilling is prominent in the two lateral units (the middle unit is not very intense). Multi-unit pant threats are the same sounds which Rowell and Hinde called "pant threats," although they did not point out that such sounds may be as trilled as one-unit threat sounds.

The above examples were chosen to illustrate that a variety of threat sounds may be generated by varying two gradients (number of units and amount of trilling). Additional variations can be produced by varying the intensity of units, the spacing between units and the length of each unit. The call which Rowell and Hinde called the "roar" seems to be a simple variant of

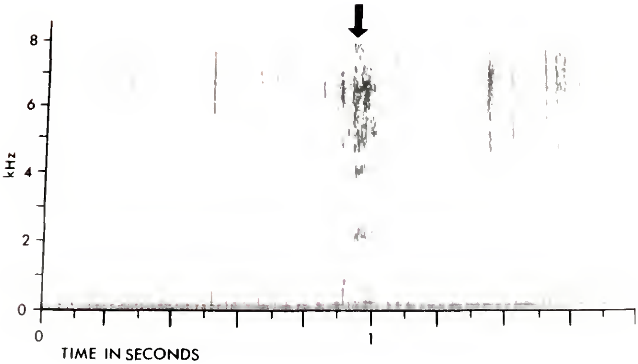

Figure 7 Spectrogram of a one-unit pant threat showing an intermediate amount of trilling.

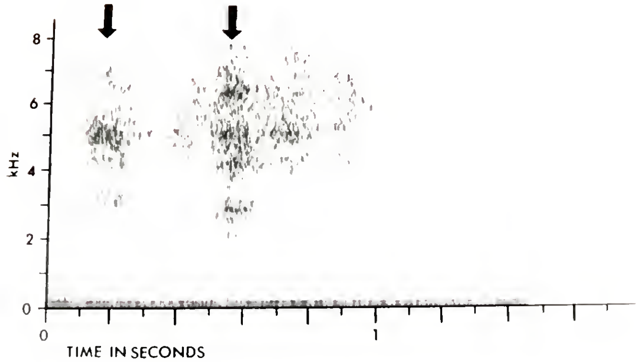

Figure 8 Spectrogram of two-unit untrilled pant threat.

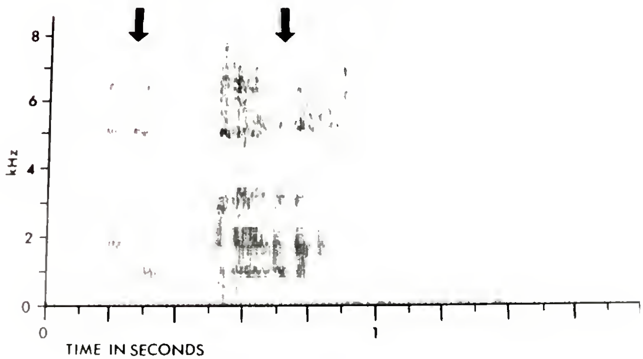

Figure 9 Spectrogram of two-unit, trilled pant threat.

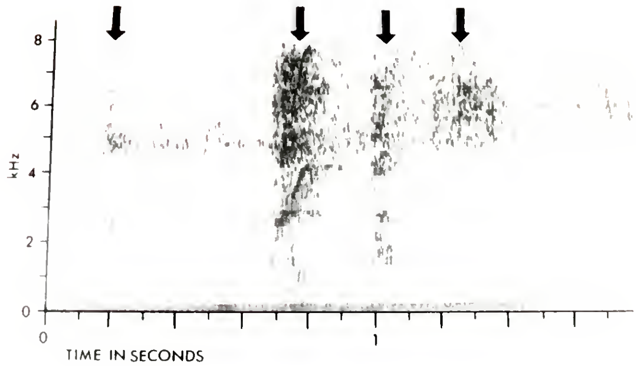

Figure 10 Spectrogram of multi-unit untrilled pant threat.

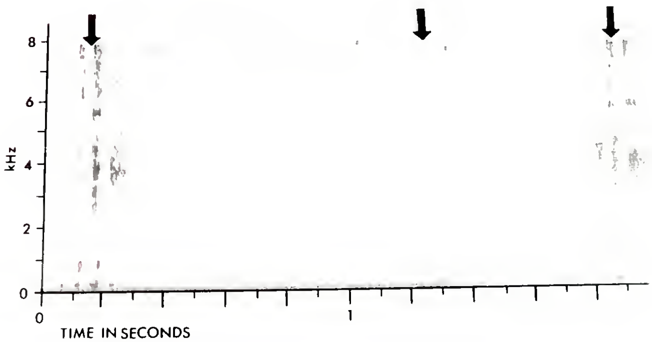

Figure 11 Spectrogram of multi-unit, trilled pant threat.

a one-unit threat sound in which both the length of the unit and the intensity of the unit have been increased. At Silver Springs, very loud, noisy sounds which were probably identical to "roars" were noted when a group of animals chased a single animal and during intergroup agonistic encounters. Although I have no samples of these sounds as emitted by a single animal (necessary for a clear spectrogram), the spectrogram published by Rowell and Hinde supports the view that the "roar" is very similar in structure to a one-unit pant threat, but longer and more intense.

Whether one chooses to retain the terminology introduced by Rowell and Hinde or to think of threat calls as a single sound with variation along multiple gradients is a matter of convenience. It is important to remember, however, that threat calls seem to exhibit only an intermediate degree of stereotypy.

Atonal Non-Threat Calls

The awkward title of this section reflects our ignorance of the emotional-motivational infrastructure of behavior which shows none of the hallmarks of threat, fear or other aversive states. Rowell and Hinde (1962) have referred to some of these calls as "friendly" and elsewhere they are sometimes referred to as "reassurance" sounds. They include noisy sounds which are emitted by rhesus monkeys in a variety of non-agonistic contexts and their common denominator seems to be that they express a relatively non-aversive emotional-motivational state in the caller and evoke no aversive state in recipients.

One of the more perplexing aspects of the rhesus auditory communication system is that sounds which are used in "friendly" contexts are so audibly

and spectrographically similar to sounds used in hostile contexts, a fact which stands in contradiction both to Darwin's principle of antithesis (1872) and Morton's motivation-structure rule (1977). There are differences, however, both in the behavior of the vocalizing animal and the response of other animals to the sound, and for this reason I have classified as separate calls some sounds which are spectrographically similar to some of the threat sounds presented in the last section. For the sake of discussion, I will distinguish three calls which will be referred to as basic grunt, purr, and chortle.

Basic grunt

The term "basic grunt" is taken from Bertrand (1969) who used it to refer to a multipurpose atonal sound emitted by captive stumptail macaques in threat, in greeting, while eating, and while exploring a new environment. Since I am reserving this term for calls emitted in non-agonistic contexts, it will be used to refer to a smaller subset of atonal calls than Bertrand's term.

Basic grunts are noisy, low to high intensity, single-unit sounds which tend to be broadcast rather than directional (i.e., they are not usually accompanied by staring). They were emitted by the rhesus monkeys at Silver Springs during periods of general, non-agonistic excitment (during feeding or in anticipation of food; before or after a river crossing), as an invitation to groom, and while looking at or touching an infant who is not an offspring or a half-sibling. They may be emitted singly or repeated in irregular trains spaced several seconds apart.

Figure 12 is a composite of grunts emitted in two food related contexts. The first grunt was emitted by an adult male while waiting for food from the

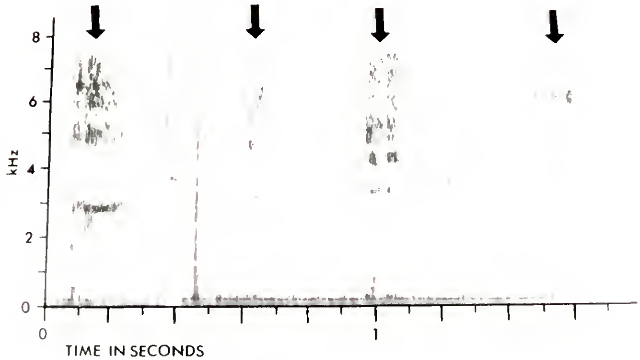

Figure 12 Spectrograms of basic grunts emitted in food related contexts.

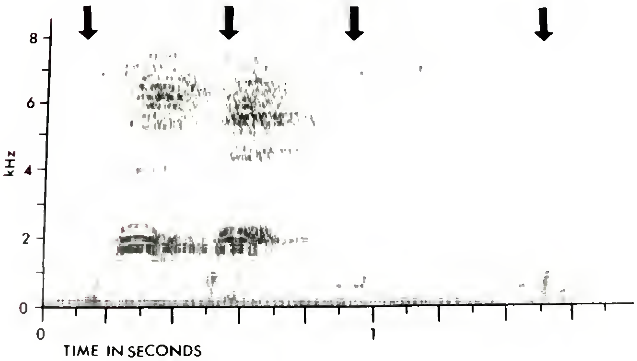

Figure 13 Spectrogram of a series of basic grunts emitted by a subadult female shortly after arriving in the vicinity of a grooming dyad. The subadult lays down and one member of the dyad begins to groom her.

investigator. The other grunts were emitted by one or more monkeys while feeding at the provisioning site. Although there is some suggestion of an energy concentration in the 3000 to 7000 Hz range, I did not find the 500 to 1500 Hz concentration of energy which Rowell and Hinde (1962) found in the call they labeled a "food bark."

In situations of general group excitment, both males and females may emit basic grunts, but more often adult males will grunt while adult females and younger animals emit the tonal call I have labeled "basic coo" (see below). Thus, the same stimulus situation provokes structually different vocal responses in different age-sex classes. Both kinds of calls may function in a feedback loop which maintains group excitment. The basic grunt is probably identical to the call Lindburg (1971) called a "bark" and which he described as "nonspecific" and emitted as "group responses during a situation of high arousal" (p. 51).

Grunts used in a grooming context are often used as elicitors of grooming from nearby conspecifics although they may also be emitted while the caller is being groomed. Some of the grunts emitted in a grooming context show a concentration of energy below 1500 Hz and there is often a suggestion of closely-spaced vertical striation (see Figure 13). Although such narrow striations are <u>only</u> seen in grooming grunts, they are not <u>always</u> present. No previous catalog of rhesus or other macaque behavior has suggested the use of a structurally similar call as an elicitor of a behavior as specific as grooming. Rowell and Hinde (1962) did, however, distinguish a call which they called the "long growl" used "in the context of initiating

grooming." I found no homologue of the "long growl" (a series of well separated, short, noisy units) in the Silver Springs rhesus colony.

The most perplexing grunts are those emitted in infant related contexts. Figure 14 shows grunts emitted by adult females who are looking at or touching an infant who is not their own. Since these sounds often exhibit a good deal of trilling, it is difficult to structurally distinguish them from the trilled sounds used in a threat context. Yet neither the infants nor their mothers react to these sounds as if they were threats and the facial expression and body posture of the caller is relaxed. Although these grunts may transit into the call known as a "chortle" (see below), they are structurally different not only in temporal delivery pattern (grunts do not exhibit the regular cadence of the chortle) but in having energy distributed fairly evenly throughout the frequency range rather than concentrated below 1500 Hz as in the chortle.

Purr

Figure 15 shows a short, trilled atonal sound which reproduces spectrographically like the trilled form of the basic grunt or the one-unit pant threat. I have classified it as a separate call which will be referred to as the purr because the volume (intensity) of this sound is stereotyped at a very low level and it seems to function neither as a threat nor as a reassurance sound.

This call was sometimes given by animals when I first arrived in the vicinity of the troop and when I fed animals, it could be heard interspersed with tonal sounds. Although a purring animal might orient in my direction while vocalizing, the same animal would immediately look away and remain silent if I looked at it, suggesting that the call did not function as a threat.

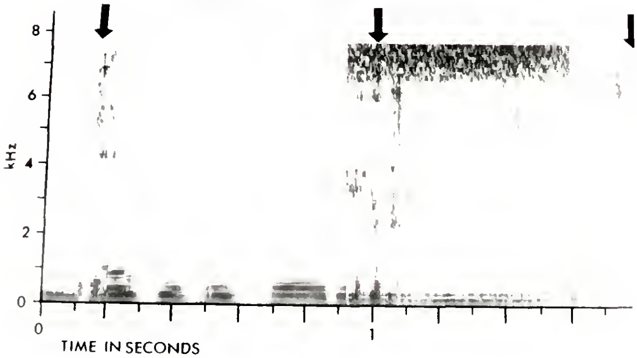

Figure 14 Spectrograms of basic grunts emitted by adult females while looking at neonatal infants of other mothers.

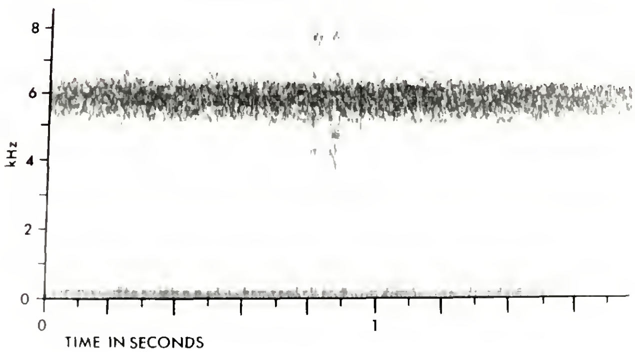

Figure 15 Spectrogram of purr emitted by a subadult female sitting in my vicinity as evening approached. (Ignore insect noise at 6000 Hz).

Purrs could also be heard interspersed with other sounds as the animals settled into their sleeping trees in the evening. The purr may express some low level of nonspecific arousal or anxiety, but it is difficult to be certain about the meaning of this call.

Although Lindburg (1971) made note of a "staccato vocalization which may be very soft, almost unvoiced," he grouped these sounds with the louder vocalization I would call a one-unit, trilled pant threat (Rowell and Hinde's "growl") and then went on to discuss the agonistic uses of this call. This may be an example of error accompanying too strict an adherence to a previously published catalog.

In a series of brain stimulation experiments, Robinson (1967) was able to evoke a vocalization which he referred to as "Krrr," a "very soft vocalization" with a "purring quality." He noted that these calls "could not be made louder or harsher by an increase in stimulus current or by external threats from the experimenter." The sound he was producing was probably the same call I have called a purr and adds weight to my argument that it should be considered a separate call from the one-unit, trilled pant threat. Altmann (1962) also categorized a call which he called "krrr" (#40 in his behavioral catalogue). His physical description of the call ("it resembles Walt Disney's Donald Duck pronouncing a soft, sustain "ōō") suggests he may be referring to a purr, but he fails to include any information about how this called is used.

Chortle

The term "chortle" was introduced by Lindburg (1971), although Rowell and Hinde (1962) first described this relatively stereotyped call and labeled it "explosive cough." Figure 16 illustrates this sound as it is emitted by a two-year old juvenile female toward a neonatal infant during the birth season. It consists of a series of short, noisy units produced in a somewhat irregular but tightly spaced cadence. Most of the energy is concentrated at frequencies below 1500 Hz. Chortle vocalizations may be accompanied by spasmodic jerking of the entire body which is very reminiscent of the jerking which accompanies the infant gecker to be described in the next section although it is not so pronounced. Often the tail is spasmodically jerked from side to side at the same time the call is emitted.

The chortle seems to be a directional call because it accompanies prolonged periods of visual staring, but it is my own feeling that the intended recipient of this call is not the infant who is the object of visual attention, but the mother of the infant. This was suggested to me when I noticed that rhesus mothers would remove their new infants from my vicinity whenever I looked at the infants for more than a few seconds. Extended visual attention without an accompanying chortle seemed to function as a visual threat, while monkeys who chortled during a period of visual attention to new infants would not evoke this protective response from mothers. The chortle, therefore, may act as a modifier of what would otherwise be a visual signal of threat (i.e., it may be an example of metacommunication).

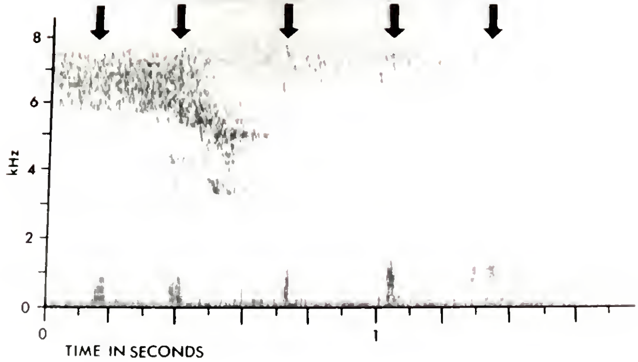

Figure 16 Spectrogram of chortling by juvenile female. (Ignore leaf rustle and insect noise at 6-8 kHz).

Most chortling is done by nulliparous females who seem to go out of their way during the birth season to crouch in front of neonatal infants and chortle. It may also be given by adult females who happen to be in the vicinity of a neonatal infant who is crawling away from its mother, and when there are several females present, a chorus of chortling may be initiated. Both the tempo and the intensity of chortling may increase if the infant seems to be in some difficulty. Mothers respond to such changes in call delivery pattern by retrieving their infants.

High-Pitched Calls

Calls which are high in pitch and predominantly atonal (although they often contain hints of harmonic structure) comprise the most structurally variable group of sounds in the rhesus repertoire. They can, however, be usefully grouped together because the facial expression of the vocalizing animals, the social context in which they are given and the response of others suggest that all but one group of these calls are imparting a fear or distress message, although other emotional (and cognitive) components may also be making a motivational contribution.

The calls in this section will be grouped into four categories: a large and highly variable group of high-pitched calls which will be referred to as "attack" calls; two calls of more stereotypic form which will be referred to as the "shrill bark" and the "gecker" (following the terminology introduced by Rowell and Hinde (1962)); a moderately variable group of calls given by males during copulation mounting.

Attack Calls

The descriptive name for this group of calls is derived from the fact that they are often emitted in response to real or anticipated attack and that they in turn often serve to rally attack against the original or suggested "aggressor." The term "attack," therefore, has a dual meaning.

Attack sounds comprise the most structurally variable group of sounds in the rhesus repertoire. As a result, they are almost impossible to fit into a typological scheme. They may be very short to very long. They may be emitted as single sounds or as long trains of highly dissimilar units extending over several minutes. The pitch may be unchanging, undulating or sharply rising and/or falling throughout the call. Energy may be distributed over a very large range of frequencies or concentrated in a narrow range. Other than noise and high pitch, there is little that these calls share structurally. Figures 17 through 20 show some of the variety possible in attack sounds.

Attack calls are emitted by females of all ages and by infant and juvenile males. The calling monkey is always subordinate to the real or alleged aggressor. Attack calls are never emitted by adult or subadult males, which may be an indication of the unlikelihood of defensive aid-enlistment in these age-sex classes. Figure 21 shows an adult female monkey at Silver Springs emitting a series of high-pitched calls after being attacked by the beta male in the southside group. Note that her mouth corners are retracted into a grimace which exposes her teeth, her body posture is tense and ready for action, and both her eyes and her body are directed at her attacker (whose attack has already ceased). This call is functioning in both a directional and a broadcast manner in the sense that it can both rally

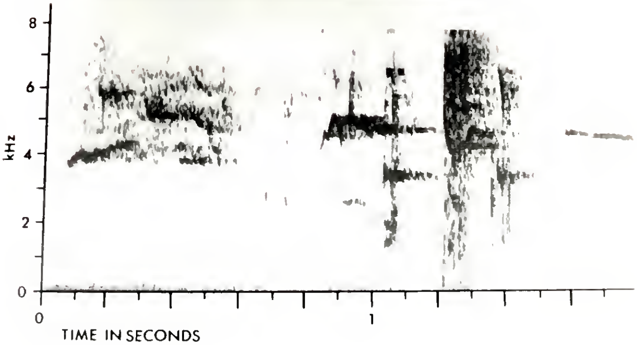

Figure 17 Spectrogram of an attack call emitted by a two-year old juvenile as it passes the investigator. The juvenile grins in passing and emits an irregular series of high-pitched units lasting 2 1/2 seconds.

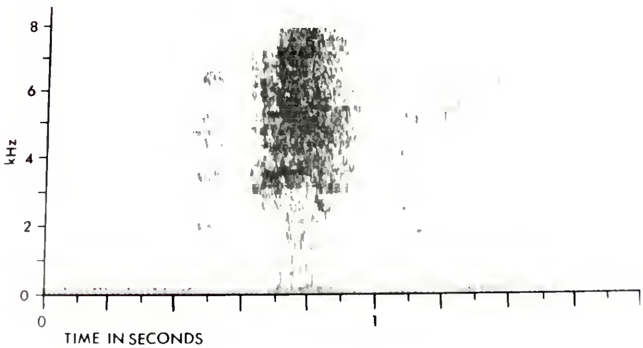

Figure 18 Spectrogram of a multi-unit high-pitched call emitted by a juvenile during a play bout. Play ceases immediately and then the caller chases the other juvenile who is older.

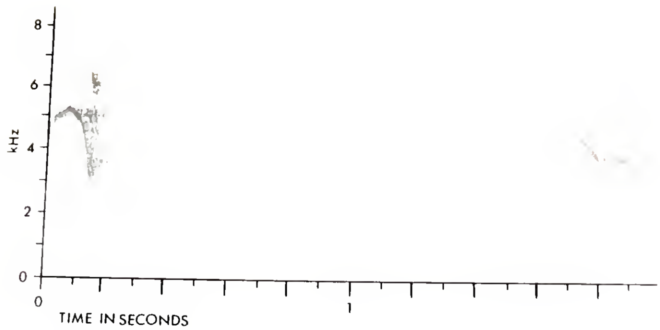

Figure 19 A one-year old juvenile is approached by a non-sibling juvenile and emits a series of high-pitched sounds, two units of which are shown. The three-year old sibling of the caller comes and sits near her and calling ceases.

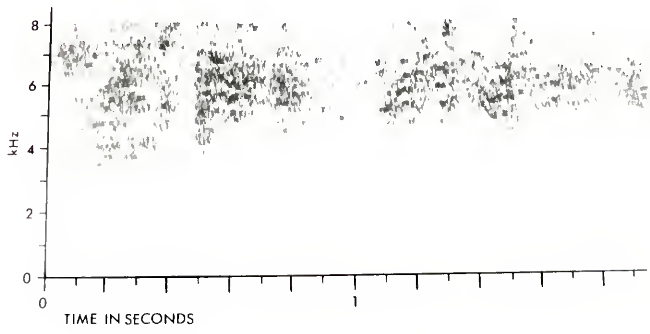

Figure 20 A one-year old juvenile who has been attacked by an adult female sits a safe distance from the attacker and emits an extended train of high-pitched sounds. Note the undulating pattern of the harmonics, some of which extend above 8000 Hz.

Figure 21 Adult female emitting an attack call.

agonistic behavior from other animals over a wide field and accurately direct them to the "aggressor." It may also stimluate the original aggressor to further attack. It may be for this reason that attack calls are more often emitted by an animal who is safely at some distance from the aggressor and rarely by an animal who is actively being chased.

Calls noted by earlier investigators which are probably within the range of attack sounds recorded from the Silver Springs rhesus colony include the call labeled "Eech" by Chance (1956), the "Ēēē" of Altmann (1962) (#36 in his behavioral catalogue), the "shriek" of Andrew (1963), the "squeak" and "screech" of Rowell and Hinde (1962), the "scream" and "gecker-screech" of Rowell (1962), the "squawk" of Lindburg (1971).

Rowell and Hinde (1962) and Rowell (1962), aided by spectrographic analysis, were the only investigators to differentiate attack calls. Unfortunately, elevating three sounds to call status does not do justice to the immense variety of high-pitched sounds which rhesus monkeys produce. Lindburg (1971), Erwin (1975) and probably numerous later observers of rhesus monkeys have accepted the Rowell and Hinde categories without allowing their ears to alert them to the impossibility of assigning all high-pitched calls into the three narrowly defined types.

Instead of trying to distinguish "types" of attack calls and assign meaning to each individual one, I would like to suggest that a single arousal continuum may be sufficient to explain all the variety evident in non-stereotyped, high-pitched calls. This arousal continuum, in turn, may dovetail with the motivational pre-disposition of listeners to determine if attack will be provoked. A brief, low intensity, high-pitched sound uttered by

an adult female (and signaling a relatively low arousal level) may bring no response from other animals but the same sound uttered by an infant may stimulate attack by the mother of that infant. A high-pitched sound which signals (via increased length and intensity) a higher level of arousal in the caller may provoke a less motivated animal to attack in defense of the adult female.

Increasing the intensity and duration of a sound is one way of signaling a higher level of arousal in the caller, but another way is to break up the sound into highly contrasting units to which rapid habituation is unlikely. It is the contrast value of producing an immense variety of high-pitched sounds which may have been the selective pressure for non-stereotyped attack sounds.

Shrill Bark

The shrill bark is a stereotyped, single-unit call which seems to function as an alarm call. The term is taken from Rowell and Hinde (1962) who reported that this call was made whenever an attempt was made to capture an animal. Lindburg (1971) described the shrill bark as a "single, loud high-pitched sound" given by adults and juveniles of both sexes in response to any known source of danger.

Figure 22 shows the structure of this sound to be wide frequency and noisy, with a major distribution of energy between 1000 and 7000 Hz and some temporal extension of widely spaced bands. The exact frequencies of these extended bands seems to vary between monkeys. The total length of this call is typically less than 250 msec.

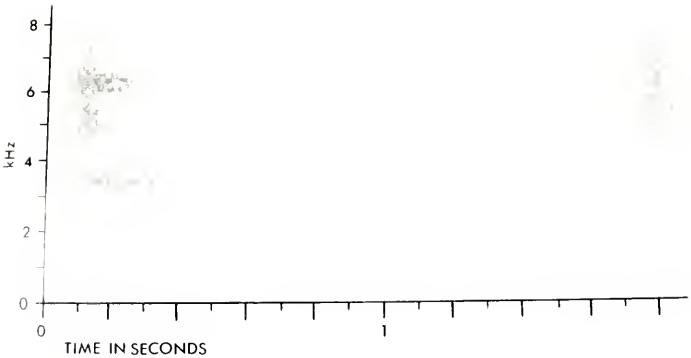

Figure 22 Spectrogram of shrill bark emitted by a subadult male in response to the sight of an alligator in the river. This call is part of a series.

At Silver Springs, the shrill bark was most frequently stimulated by the sight of an alligator approaching the riverbank. It is given in long trains while the vocalizing animal sits in an overhanging tree branch and looks in the direction of the stimulus. The response to this call is variable. Some monkeys will flee immediately into the trees, especially if the caller is nearby, others may react with a startle and then scan the environment. Distant calls may be completely ignored.

Warning calls are also given by the monkeys in response to the approach of humans on land (but not to humans who approach by river as long as they remain in their boat). In this situation, the call is a single, brief sound which stimulates rapid flight into the trees. As well as being different in temporal delivery than the gator call, this warning call sounds like it may be different in structure but I am unable to verify this because of the difficulty of recording it. This call seems to be homologous identical to the call which Altmann (1962) called " !Ka! " (#55 in his behavioral catalogue) and which he described as given in response to the sudden approach of a human observer.

Gecker

The gecker is a relatively stereotyped staccato emitted by infants and juveniles and accompanied by spasmodic jerking of the body. Altmann (1962) labeled this call "Ik, ik, ik . . . " (#24 in his behavioral catalogue) and noted that it was commonly given "by infants in frustrating situations, e.g., when being weaned." Rowell and Hinde (1962) introduced the term "gecker" and also noted its association with the interruption of suckling. Lindburg (1971) suggested additional stimulus situations for infants and juveniles, including maternal restraint, departure and punishment.

Figure 23 shows the structure of this call to be a series of unevenly spaced units with most of the energy concentrated between 3000 and 7000 Hz. The vocalizing animal has a grimace on its face which exposes the teeth and the entire body jerks as the call is emitted. At Silver Springs, geckers were often emitted by juvenile animals after maternal rebuff. The gecker may represent some modification of an attack call, given in a situation in which aid-enlistment is precluded.

Copulation Calls

Calling during copulation was rarely observed among female rhesus monkeys during the mating season at Silver Springs but calling by resident males occurred with appreciable frequency. Solitary males, on the other hand, were never observed to emit calls during copulation. Surprisingly, the only cataloguer of macaque sound signals to note the presence of calls during copulation was Altmann (1962, p. 381), although he believed them to be structurally identical with the call he called "Eee" (#36 in his catalogue) which he ascribed to fearful, submissive animals.

Copulation calls are brief, high-pitched and usually single-unit calls (although several very short units can be distinguished in some spectrograms). All of my samples were less than one second in length but the calls were quite variable both in structure and intensity. Figures 24 and 25 show calls emitted by two different males in the southside group. Figure 24 shows a narrow frequency, squeaky sound which was also of relatively low intensity. Figure 25 shows a wide frequency call emitted by the alpha male. Many of the calls emitted by the alpha male during copulation were extremely loud and could be heard an appreciable distance away, even when the copulating

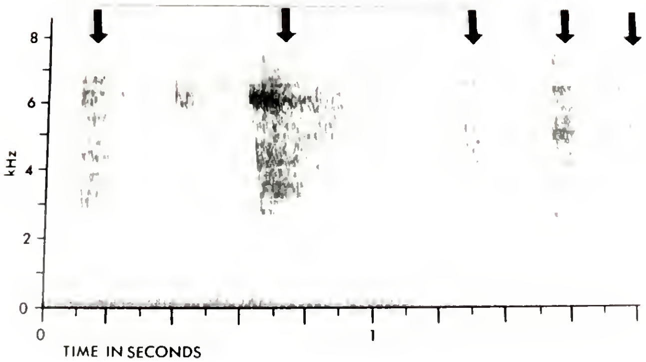

Figure 23 Spectrogram of five units of a six-unit gecker emitted by a one-year old monkey.

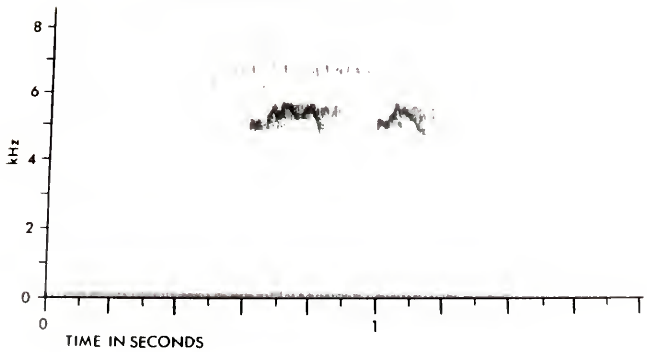

Figure 24 Spectrogram of copulation call emitted by a resident adult male.

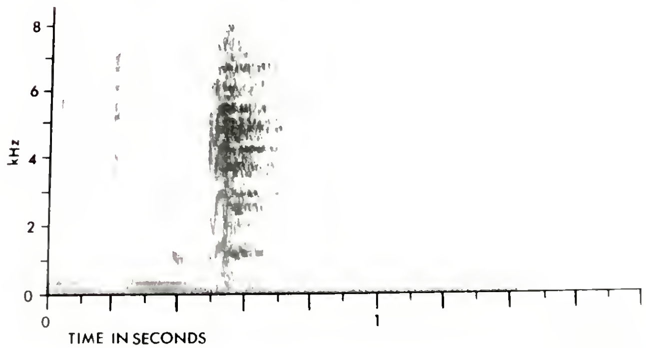

Figure 25 Spectrogram of copulation call emitted by the alpha male.

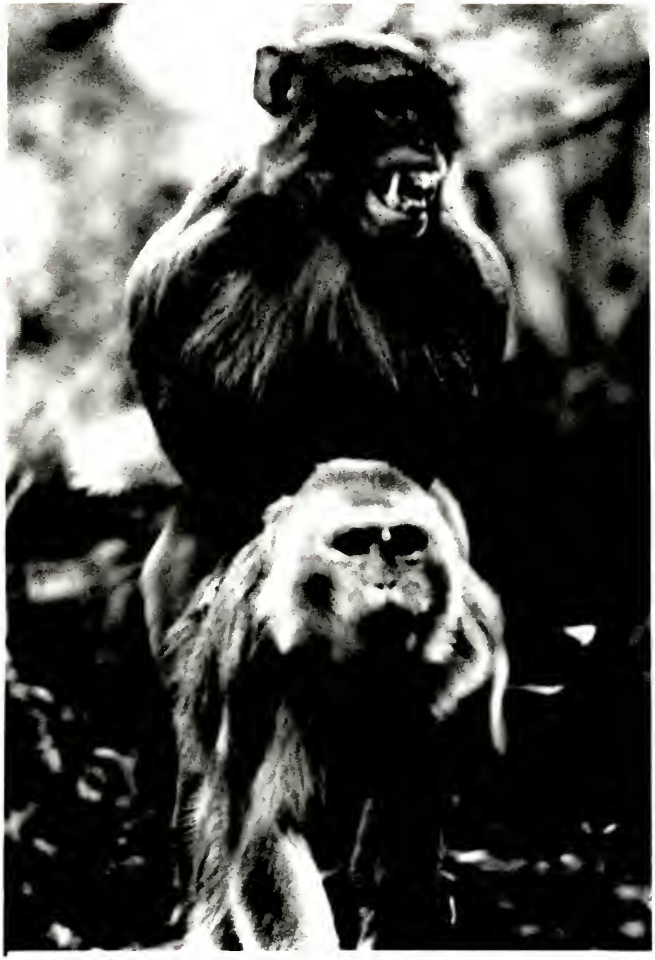

Figure 26 Adult male emitting a copulation call.

monkeys were themselves out of sight. All copulation calls were accompanied by an extreme grimace (as shown in Figure 26), although I also observed the grimace during pre-ejaculatory mounts when no sound was emitted. Calling was never noted during the ejaculatory mount.

Categorization by form alone would dictate a merger of these calls with the high-pitched calls described earlier, but since they seem to function in a manner which is completely different, they warrant separate consideration. Since the calling animal seeks to turn on the stimulus which is associated with emission of the call, these calls do not seem to signal an aversive emotional-motivational state. Copulation calls seemed to be ignored by other animals in the vicinity of the consort pair.

Tonal Calls

Calls which are notably tonal in structure comprise an audibly distinctive group of rhesus sound signals. Most (but not all) are relatively short sounds (less than 500 milliseconds long) with energy concentrated in one or more continuous and fairly linear bands. They may be emitted as single events or as trains of irregularly spaced units, usually without accompanying visual signals (in contrast to threat or fear calls). At Silver Springs, tonal calls were frequently emitted by adult and subadult females and by juveniles and infants of both sexes. They were infrequently emitted by adult and subadult male members of the southside group and were never noted in solitary males.

Chance (1956) apparently lumped all tonal calls into the single category which he called "Coo-Coo." Altmann (1962), similarly, distinguished a single "legato, whistle-like vocalizations" which he designated "Kōō" (#56 in his behavior catalogue) and Andrew distinguished a single tonal sound which he labeled "woo." While Reynolds (1976 (1961)) suggested that "wailing" could be discriminated from "food call," Rowell and Hinde (1962) refrained from cataloguing tonal calls and presented, instead, a list of situations in which tonal calls were emitted.

The major splitting of tonal calls was accomplished not on the vocalizations of rhesus monkeys but on the vocalizations of congeneric pig-tailed macaques (Grimm, 1967) and Japanese macaques (Green, 1972, 1975).

Grimm (1967) distinguished 12 kinds of tonal sound signals, but gives very little information about associated behaviors. He also notes that "no one monkey . . . has used the 12 calls defined," which leaves open the possibility that some of the sound discriminations which he made were the result of individual rather than situational differences, a subject that will be explored in greater depth in the next chapter. It may also be relevant to note that some of the tonal calls which Grimm distinguished in his laboratory animals (e.g., the "leap coo") look suspiciously similar to the tonal calls which Newman and Symmes (1974) cited as evidence of vocal pathology in socially deprived monkeys.

The most intensive effort to discriminate differences in the tonal calls of a macaque monkey and relate these differences to social context was made by Green (1972, 1975) in his field study of Japanese macaque monkeys.

He distinguished 7 types of tonal calls, based on minor variations of acoustic form, and 10 social situations in which these coos were emitted.

The rhesus monkeys of Silver Springs were only observed to emit tonal calls in three social situations which could be equated with the social situations presented by Green. These were "young alone," "dispersal," and possibly, "young to mother." I did not perceive tonal calls in association with the situations which Green labeled "female minus infant," "nonconsorting female" (but there was one set of calls by a "nonconsorting male"), "female at young," "dominant at subordinate," "subordinate at dominant," or "estrus female." In the case of "female minus infant," this may reflect a difference in sampling since the death of an infant did not occur during my observations. For the other social situations, the absence of tonal calls may reflect a real difference in the vocal behavior of Japanese macaques and rhesus monkeys. Rhesus monkeys may not have evolved as many social uses for tonal calls as have Japanese macaques.

With one exception, I did not find it useful to sort spectrograms of tonal calls using the criteria established by Green for the tonal calls of Japanese macaques. This may be related to the finding of Zoloth et al. (1977) that Japanese macaques can more easily learn a discrimination based on the position of the peak frequency while rhesus monkeys can more easily learn a discrimination based on starting pitch. Many of the distinctions which Green made between tonal calls were based on changes in frequency over the temporal course of the call, a feature which may be less meaningful for rhesus monkeys. It may also be relevant to note that the spectrograms which Green published of Japanese macaque tonal calls show less dispersal of

energy into the higher frequencies than I found in my spectrograms of rhesus calls. Rhesus monkeys and Japanese macaques may have evolved slightly different emphases in the manipulation of parameters for producing different types of calls.

In cataloguing tonal calls, I distinguished six different types of calls which were both audibly and spectrographically distinct. These will be referred to as basic coo, elongated coo, emotive coo, mewing, abbreviated coo, and girning.

Basic Coo

This is the most frequent tonal call given by adult and subadult females and by juveniles of both sexes. Figure 27 shows three examples of spectrograms of these calls as emitted by three different animals in response to the same stimulus situation. Figure 28 shows an adult female member of the southside group emitting a basic coo in response to the sound of a motor boat, a sound which has become a conditioned stimulus heralding the arrival of provisioned food. Note that while the front of the mouth protrudes forward, the corners are pulled back slightly creating a moderately wide mouth opening but with teeth covered. The body posture is relaxed, and the call is broadcast rather than directed at a particular individual.

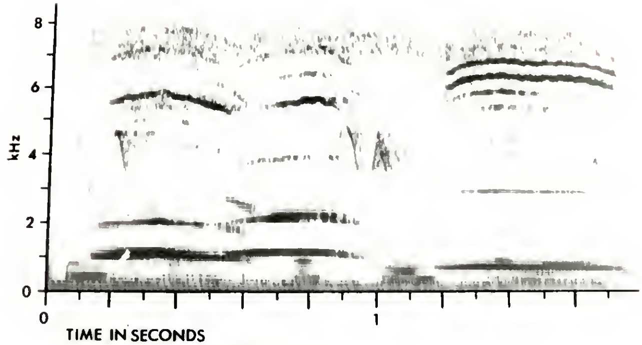

Figure 27 Spectrogram of basic coos emitted by three sibling juveniles in response to the sound of a motor boat.

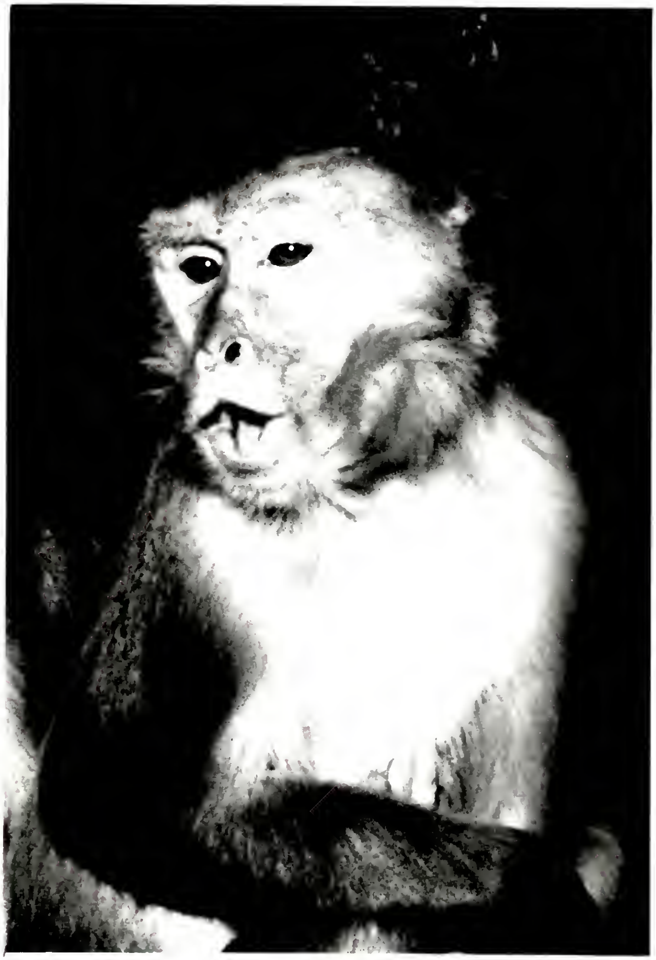

Figure 28   Adult female emitting a basic coo.

Basic coos are emitted in two social contexts which can be summarily described as "general excitment" and "dispersal." Periods of generally non-hostile group excitment (which could, however, spill over into agonistic behavior) were noted by this investigator surrounding the daily delivery of provisioned food and preceding any river crossing (a river crossing necessitated swimming across the alligator infested Silver River or locomoting under a high wire which happens to be strung across the water). During such periods the monkeys become very vocal with the high intensity coos of some monkeys alternating with the grunts and high-pitched sounds of others. Such coos are often emitted in irregular trains and seem to be both stimulated by the vocalizations of others and to provide feedback stimuli which maintain group excitement.

Basic coos were also emitted during periods of relaxed dispersal by monkeys who were foraging, grooming or merely sitting quietly. Such calls are often single events or a brief series of widely spaced units. They may be stimulated by the emission of a basic coo by another (usually out of sight) animal or the stimulus may be unclear. Whether emitted by relaxed or excited monkeys, a key feature of these calls is that they are non-directional.

Lindburg (1971) has suggested that tonal calls given during foraging by forest-dwelling monkeys in India may be used as position markers and to maintain contact when the group is widely dispersed. Green (1975) has suggested that all the tonal sounds can be described as functioning in "affinitive contact" situations. This investigator believes that the basic coo, and perhaps other tonal sounds, also function as identity sounds, a topic which will be developed in greater depth in Chapter 4.

A key feature of the basic coo (and one which contrasts this call with the other tonal calls described in this section) is that it seems to be extremely susceptible to social facilitation. Although the sound of the provisioning boat coming down the canal typically provokes basic coo chorusing over a broad radius, similar motor sounds such as other boats on the river or low-flying airplanes do not usually provoke this response. However, if a single monkey fails to make the discrimination and emits a basic coo in response to these latter sounds, other monkeys often follow suit. This suggests that the calls themselves function as social stimuli for further calling and that the calling is not just a common response to a non-social stimulus.

Elongated Coo

Elongated coos are tonal sounds which resemble basic coos in the overall distribution of energy, but are distinguishable by temporal length. While basic coos are generally no more than 500 msec. long, elongated coos are 1000 msec. and longer. All of my samples of this call come from a single unusual situation.

Strung across the Silver River, at a point about 3/4 of a mile below the headsprings and about 50 feet above the river, is a heavy gauge cable wire (originally erected as a movie prop). On several occasions, I observed the southside group use this wire to cross to the north bank, but use of this route requires the monkeys to hang under the wire with all four limbs and use a progression technique which is not part of the normal locomotor repertoire. The first time the southside group was observed crossing this wire, two adult females were either unwilling or unable to negotiate this route and remained

on the south bank with their respective infant offspring. As most of the southside monkeys moved out of sight on the north bank of the river, one female remained relatively quiet, but the other began an intermittant train of elongated coos, one of which is reproduced in Figure 29. Although there was no obvious immediate response to these vocalizations (which extended intermittantly over a period of two hours), shortly before darkness set in for the evening, the two juvenile offspring of the calling female re-crossed the wire and were later observed in a sleeping huddle with their mother. Whether the female's calling had some instrumental effect on the behavior of the offspring is unclear.

The only homologue of the rhesus elongated coo which has been catalogued by previous researchers is the "long coo" of the pigtail macaque (Grimm, 1967). Unfortunately, Grimm gives no information about the context of this call.

Emotive Coo

Figure 30 shows two examples from a series of calls uttered by a subadult female during a period of separation from her troop. The term emotive coo is taken from Grimm (1967), although examination of the spectrogram which he published suggests that the pigtail call may not be the exact structural homologue of the rhesus call. Grimm does note that the pigtail call occurs in animals which have recently been separated from conspecifics, that it has a "mournful and evocative" timbre and that it tends to evoke "sympathetic responses from humans," all features which accurately describe the rhesus call heard at Silver Springs. Rowell and Hinde (1962) noted that "clear calls" were emitted by animals "shut away from their cage

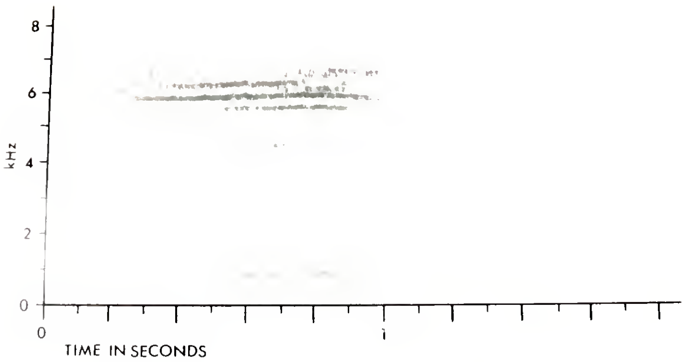

Figure 29 Spectrogram of an elongated coo emitted by an adult female left behind when the group crossed by wire to the north bank of the river.

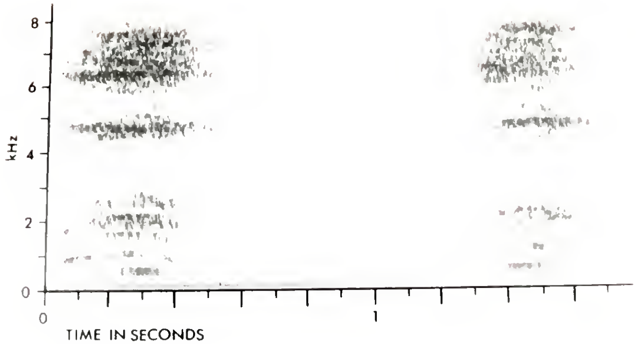

Figure 30 Spectrogram of two emotive coos emitted by a subadult female during a period of separation from the group.

mates" but the two spectrograms which they published do not show any evidence of the noisy and rich harmonic structure of the emotive coos emitted by the Silver Springs monkeys and also characteristic of Grimm's spectrogram. The emotive coo is undoubtedly identical to the "lost call" which Lindburg (1971) described for forest-dwelling rhesus in northern India.

This call was first noted at Silver Springs when a subadult female became separated from the southside group as it moved downriver and out of visual and auditory range. The female moved about aboreally in an erratic manner and seemed to be scanning the surroundings visually between calls. The calls were usually emitted as single units with 10-20 second pauses between units, but intermittantly trains of three calls were emitted in rapid succession. This same pattern of arboreal movement interspersed with calls were also noted one evening during the mating season in an unfamiliar subadult female who was discovered to be alone as evening approached. After calling continuously for more than half an hour, the female was joined by an unknown adult solitary male and the calling ceased.

Emotive coos were the only tonal calls which I ever heard from adult male members of the southside group and these were only emitted in a few unusual circumstances. On one occasion during the mating season, the beta male in the group was found sitting alone in a tree emitting emotive coos. In contrast to the "lost" subadult females described above, this male did not move about and his posture was relatively calm (depressed?) as indicated in Figure 31. Earlier that day, this male had been seen in consort with an adult female member of the group and shortly after the calling bout he rejoined the

Figure 31 Adult male emitting emotive coo during a period of separation from his consort.

female. On two occasions, the emotive coo was emitted by the alpha male as he sat in a tree located several hundred feet downriver from the adult female members of the group. On both occasions the progression of the group downriver was apparently halted by the failure of the core of adult females to follow in the direction initiated by the alpha male.

The emotive coo seems to correspond to the "double coo" which Green described for Japanese macaques ("double" refers to the fact that there may be two overlapping harmonic series in the call). Green described this as a call given by adult females in conjunction with the death of an infant and by solitary males who have been left behind when a troop retires from the provisioning area during the mating season. As noted previously, I am unable to verify the use of this call by mothers experiencing the death of their infant. I never heard an emotive coo or any other vocalization from any of the solitary males who were frequently seen in the vicinity of the southside troop during the mating season.

Mewing

Mewing is wide-frequency tonal calling often with a warbling frequency course. All of my samples of mewing come from infants and young juveniles, so it is basically a call of immature animals. Although this call is widely referred to in the literature as a "coo," it is sufficiently distinctive in audible quality, delivery pattern and social usage to warrant a descriptive label which is different from that used to refer to the most frequent tonal call of older animals. The term "mewing" is taken from Kaufmann (1966) who used it to describe tonal calling by young infants of the Cayo Santiago rhesus colony.

As indicated in Figure 32, the mew call is similar to the basic coo in being composed of a series of tonal bands with a relatively even distribution of energy among the bands. The wider spacing of the bands gives this call a thinner quality and higher pitch than the basic coo, while the warbling gives this call a special "irritating" effect (discussed below) which contrasts with the pleasant (to human ears) effect of the basic coo. A final contrast between the basic coo and the mew call is the pattern of temporal delivery. Basic coos usually exist as single events, although during periods of excitement (e.g., when provisioned food is delivered) repeated cooing may be heard. Mewing, on the other hand, is usually emitted in long trains which may last 30 minutes or more. On one occasion, I counted a succession of 138 mew calls from an 8-month old infant within a twelve-minute period. Mew calls are sometimes interspersed with high-pitched calls and geckers, and the entire sequence seems to be indicative of fluctuating levels of distress.

Figure 33 shows an infant emitting a mew call. Note that the infant's mouth is rounded, as Lindburg (1971) has pointed out, into a "distinct O" in contrast to the wider mouth opening in the adult basic coo. This plate shows the infant in a relatively relaxed posture as the call is broadcast, but I have also noted infants mewing in an almost absent-minded manner as they were otherwise occupied in object exploration or climbing about in tree branches.

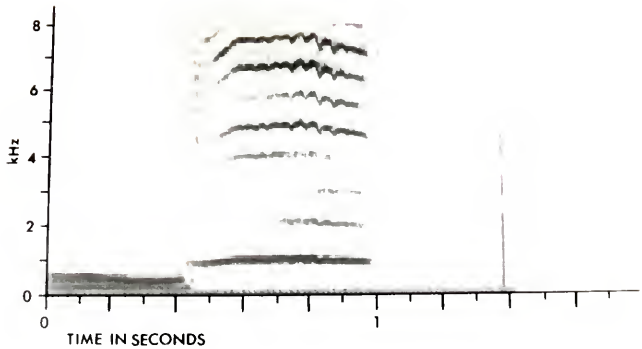

Figure 32 Spectrogram of mew call emitted by an infant.

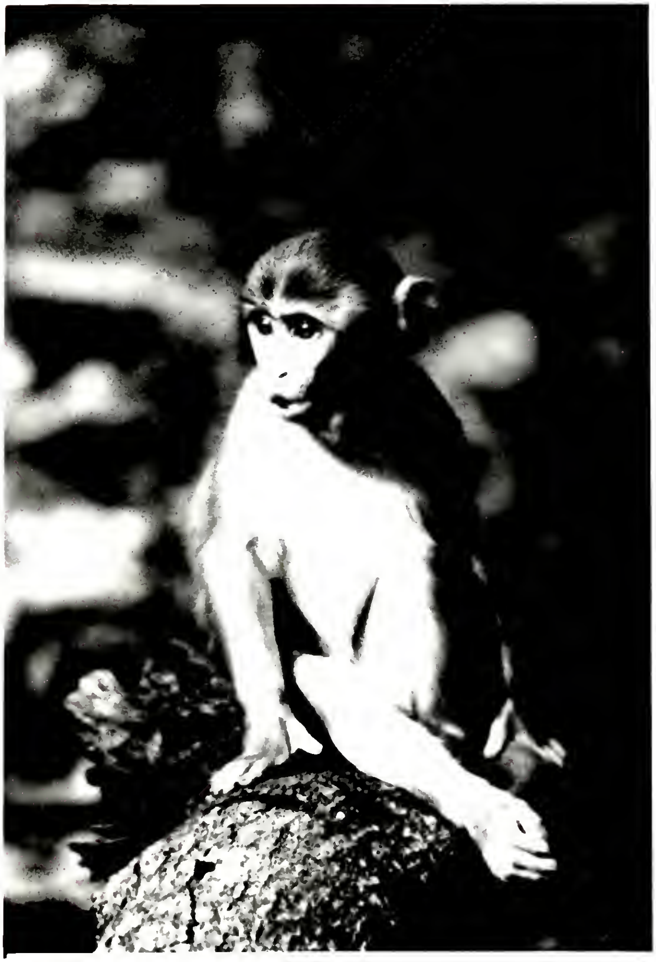

Figure 33 Eight-month old infant mewing.

Much mewing seems to be related to weaning as the vocalization is often initiated by an interruption of nursing and is sometimes accompanied by the infant actively trying to regain access to the nipple. If the goal is achieved, mewing stops. Most of the time, however, mewing seems to accompany whatever activity the infant happens to be engaged in. Although a mewing infant occasionally attracts the attention of a nulliparous female, more often the extended trains of mewing evoke no response from other monkeys.

I have heard infants mewing after darkness descended when the rest of the group is relatively quiet. On one occasion during the mating season a solitary male approached with lip-smacks and seemed to be using the incessant mewing of the infant as a means of locating and re-locating the mother despite her repeated change of position.

Long trains of mewing are irritating for human observers to hear and it is possible that the call evolved because it is irritating for rhesus mothers to hear these sounds as well. Erwin (1974) has suggested that ". . . it seems likely that cessation of such sounds is reinforcing and that mother monkeys learn to refine their maternal behavior by learning techniques of rapid 'escape', i.e., by responding immediately to the infant vocalization in some fashion which has a high probability of turning off the sound" (p. 179). At Silver Springs, the frequency of mewing by infants in the presence of their mothers suggests that mothers are not always induced to "turn off the stimulus" by allowing nursing. The evolution of this kind of tonal calling may represent an example of "parent-offspring conflict" (Trivers, 1974). The advantages of weaning to the mother may be in conflict with the advantages

to the infant of continued access to the nipple and mewing may be an infant strategy for prolonging access.

Abbreviated Coo

Abbreviated coos are very brief, extremely low volume sounds which were only noted in a single situation. This, however, is probably the result of sampling bias and may not reflect the full range of their use since they probably went undetected in animals more than a few feet away. These sounds were uttered by adult and juvenile females who were sitting in my immediate vicinity as I distributed food. They were emitted by these animals during eating or while anticipating a food distribution, and they might be interspersed with basic coos. One subadult female uttered these calls very frequently in this context, while I rarely or never heard this call from other animals.

Abbreviated coos sound almost like effort noises and it is only upon spectrographic analysis that their basically tonal structure becomes apparent. Figure 34 shows two examples of an abbreviated coo given in rapid succession by the same adult female. Although there is some emphasis of the lower frequencies in this sound, energy tends to be distributed over a wide range of frequencies. Abbreviated coos may represent some variant of the basic coo in which arousal is insufficient to produce the longer sound. They may be homologous with the "short coo" which Grimm (1967) distinguished for pig-tail macaques and which he noted as "uttered by idle monkeys" and "easily overlooked." Green (1975) distinguished a similar looking call in Japanese macaques which he called "Ech" sounds and which were given when a "very

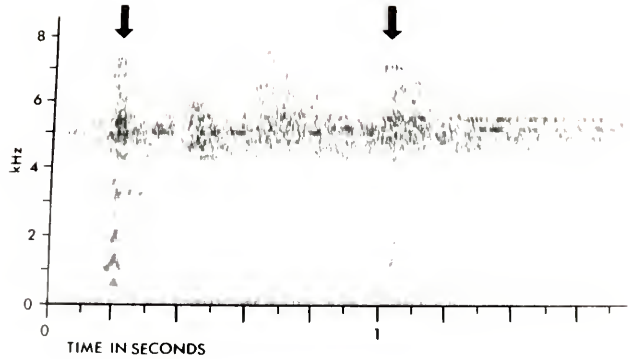

Figure 34 Spectrogram of abbreviated coo emitted by a subadult female.

transitory arousal of the vocalizing monkey decays into a more calm state" (p. 49).

Girning

The term "girning" was introduced by Rowell and Hinde (1962) who used it to describe a low intensity nasal whine used by the animals in their captive colony immediately after release into an outdoor run and when approaching and joining another animal. The spectrograms which they published showed this sound to be about 500 msec. long and made up of a series of closely spaced frequency bands with a concentration of energy below 2000 Hz.

Figure 35 shows a representative sample of girning as emitted by an adult female in the Silver Springs rhesus colony. The closely spaced harmonics and the low intensity of emission resemble these same features of the Rowell and Hinde call, but contrasting features include a wide frequency distribution of energy and a warbly frequency course. The temporal duration of this call is extremely variable; calls of this structure have been recorded which are as short as 250 msec. and as long as 6 seconds.

Rowell and Hinde (1962) described girning as a "pleasure noise" which is made "only by contented animals," but the range of contexts in which girning was noted at Silver Springs make this interpretation too narrow. Girning was emitted by adult animals (both male and female) just prior to pulling an infant into a ventral carrying position. In one case, the beta male (who had developed a protective relationship with a yearling male) girned as the alpha male approached and then the beta male carried the yearling out of the path of the alpha male. During the wire-crossing incident described in a previous section, an adult female girned as her infant started locomoting across the

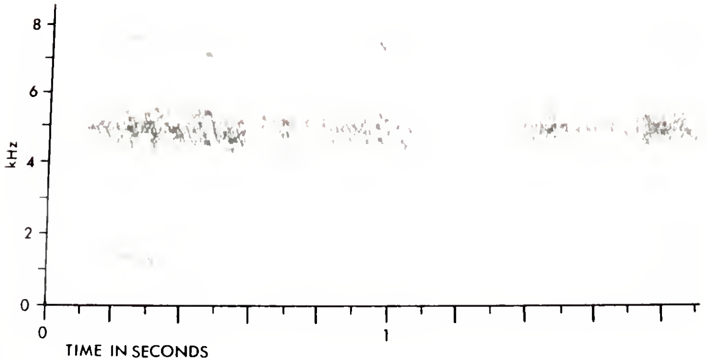

Figure 35 Spectrogram of girning by an adult female. (Ignore insect noise at 5000 Hz).

river on the wire with the result that the infant locomoted back toward her and was pulled to her ventrum. Juveniles have been heard girning after completing a pant threat sequence or during a social mounting sequence among juvenile and subadult males. Juvenile females have been heard girning while looking at neonatal infants. Girns may be interspersed with grunts and coos during provisioning. Thus, while girning seems to signal motivation for positive affinitive contact, it may be something other than or more than a "pleasure noise."

Green (1972, 1975) made note of a structurally similar call in Japanese macaques which he called a "whine." He observed that it was used by animals "after a weaning tantrum, after being lost or abandoned, and after losing a fight." No other researchers have catalogued a sound which resembles the mulatta and fuscata calls.

Typologies Compared

A typological overview of the rhesus repertoire is presented in Table 3 which compares the call categories delineated in the present chapter with those suggested by previous investigators studying other colonies of rhesus monkeys. While this table compactly summarizes the analytic results of multiple investigators, it should be referenced with extreme caution for three reasons. First, the call categories defined by previous investigators were not always easy to equate with my own categories. For example, the "basic grunt" I defined is a broader category than the "food bark" of Rowell and Hinde (1962), while the "growl" of Lindburg (1971) seems to include sounds which I would assign to two of my own call categories. In some cases, I had

Table 3: A comparison of call typology by seven investigators of rhesus vocal communication.

Peters, 1983	Rowell and Hinde, 1962 Rowell, 1962	Chance, 1956	Reynolds, 1976 (1961)	Altmann, 1962	Lindburg, 1971
Atonal Threat					
one-unit pant threat	bark		hough	!Ho!	bark
	growl				growl
	roar				
two-unit pant threat					
multi-unit pant threat	pant threat	hough-hough			pant threat
Atonal Non-Threat					
basic grunt	food bark		feeding hough		
purr				Krrr	
chortle	explosive cough		explosive cough		chortle
	long growl				
				Hu, hu, hu	
				!Ka!	
High-Pitched					
attack calls	screech	eech	screech	Eee	screech
	gecker-screech		geckering-screech		
	scream		scream		scream
	squeak				squeak
					squawk
		ee-o			
shrill bark	shrill bark		bark		shrill bark
gecker	gecker		gecker	Ik, ik, ik	gecker
copulation calls				Eee	squeak
Tonal					
basic coo	clear call	coo-coo	food call	Koo	calls
elongated coo					
emotive coo					
mewing			wailing		
abbreviated coo					
girning	girning				girning

difficulty finding any equivalent to a previously defined call and in all cases the equivalences should be considered tentative since they were not made in consultation with the investigators listed. A second reason for caution in referring to this table is the unevenness in breadth and stereotypy, even in those categories defined by a single author. The "one-unit pant threat" I defined, for example, comes in a variety of forms, while the "shrill bark" is relatively stereotyped. Reference to the discussion of each call presented in this chapter makes this clear, but listing in a table obliterates this important point. Finally, I emphasized at the beginning of this chapter that typological thinking alone is not only inadequate for describing the rhesus repertoire, it may actually interfere with our understanding of the system which underlies the production of specific calls. An alternate way of thinking about form-meaning relationships will be developed in Chapter V.

CHAPTER IV

INDIVIDUALIZATION IN THE BASIC COO

Researchers conducting long-term research with rhesus monkeys (or other species of non-human primate) are quickly impressed by the visual uniqueness of individual animals. This uniqueness of visual appearance (which transcends age and sex markers) has been used by researchers as the basis for assigning identifying names or numbers. Primatologists can often avoid the trauma of capturing and marking their subjects which other field biologists find essential to the collection of accurate data about individuals. The widespread practice of visually identifying individual field subjects has, in turn, facilitated the collection of data confirming individualized social interactions among group-living animals. The animals, like their human observers, seem to be using markers of individuality to discriminate between conspecifics and adjust their behavior. Variability between individuals makes possible such important individualized behaviors as parent-offspring bonding, collateral kin recognition, group membership identification and dominance relations.

While working with the southside group at Silver Springs, I was impressed with the ease with which I was soon able to assign samples of the most frequently heard tonal call, the basic coo, to individual animals. This call seemed to be both variable between individuals and relatively stereotyped within individuals (i.e., it was as individualized as the animal's physical

appearance and could be used to identify individuals in the same way that visual appearance could be used).

If the basic coo of rhesus monkeys is an individualized call, then it should be possible to discern specific features in the acoustic structure of the call which vary between individuals yet are relatively stereotyped within individuals. In an effort to determine whether such features could be detected in the calls of the southside monkeys, the spectrograms produced from a sample of basic coos were quantitatively analyzed and compared.

As noted in the previous chapter, the basic coo is emitted in a variety of social contexts. To be certain that the call under investigation was the same from individual to individual, I used only calls emitted in a single behavioral situation, in this case the calls emitted by the monkeys in response to the distribution of provisioned food. To avoid confounding markers of individuality with markers which maybe be related to age and sex, only the calls of adult female animals were selected for analysis. The three females whose calls were selected for quantitative analysis were chosen simply because more usable samples of their coo calls were available on my tapes. Even so, my sample of usable calls is small since I did not specifically collect data to test this hypothesis and the high degree of extraneous noise in the Silver Springs environment made many of the recorded calls unsuitable for analysis. The following analysis is based on a sample of four calls from the female known as VG, five calls from the female known as KA and five calls from the female known as AN. These animals were estimated to be 5, 6 and more than 10 years of age respectively at the time of sampling.

Figures 36, 37, and 38 show a representative basic coo emitted by each of three females. Structurally, this call consists of a series of narrow bands, with a fairly uniform distribution of energy in each band throughout the frequency range. There is often a slight rise in the frequency of most bands just after the beginning of the call and a slight drop just before the end of the call.

Examination of the spectrograms and the experience of other researchers on this topic suggested five acoustic parameters which might be usefully examined for evidence of individualization. The parameters examined were: total duration of the call; number of bands; start frequency of the dominant band; mid-point frequency of the dominant band; end frequency of the dominant band. Table 4 provides a description of each parameter. Measurements were made to the nearest 0.5 mm. For the sample of calls from each female, the mean and coefficient of variation were computed for each variable. These descriptive statistics are summarized in Table 5.

To ascertain whether the mean values derived for the calls of each female suggest that the samples were drawn from the same population or from different populations (i.e., whether the interindividual variance in call structure is greater than the intraindividual variance), a univariate analysis of variance (F-test) was performed for each of the five variables. The results of these analyses are summarized in Table 6.

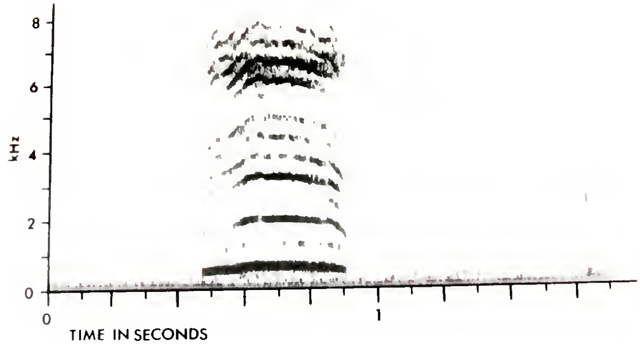

Figure 36 Spectrogram of basic coo emitted by adult female (VG).

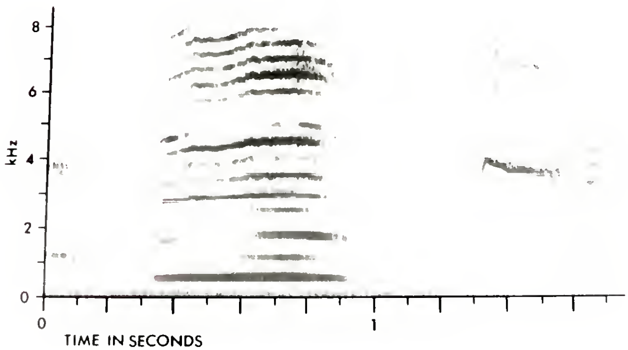

Figure 37 Spectrogram of basic coo emitted by adult female (KA).

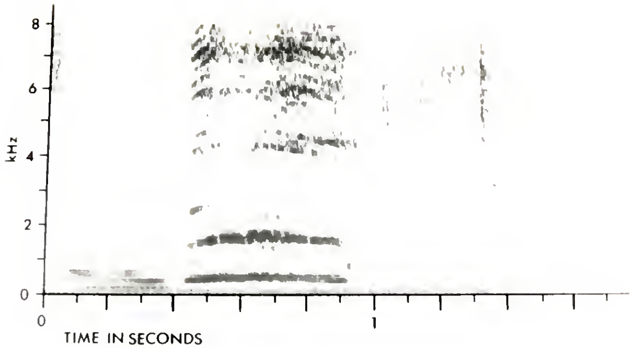

Figure 38 Spectrogram of basic coo emitted by adult female (AN).

Table 4: Acoustic parameters subject to quantitative analysis.

Parameter	Description
Duration	Maximum duration of the vocalization from the start of the first energy band to the end of the last band to show energy (exclusive of echoes).
Number of Bands	The number of visible bands at the beginning of the vocalization (an effort was made during spectrogram production to maximize the visibility of bands).
Start Frequency of the Dominant Band	The frequency measurement at the beginning of the lowest band. In the basic coo, this band is also among the blackest bands.
Mid-Point Frequency of the Dominant Band	The frequency measurement at the mid-point of the lowest band.
End Frequency of the Dominant Band	The frequency measurement at the end of the lowest band.

Table 5. Mean and coefficient of variation of five parameters of the basic coo as measured in calls generated by three adult female members of the southside group.

Animal Estimated Age	VG 5 years old		KA 6 years old		AN More than 10 years old	
	Mean	Coefficient of Variation	Mean	Coefficient of Variation	Mean	Coefficient of Variation
Duration (in milliseconds)	546	29.54	483	24.19	448	14.24
Number of Bands	13.25	11.32	15.60	3.51	18.00	4.54
Start Frequency of the Fundamental (in Hz)	500	8.25	493	3.57	336	17.8
Mid-Point Frequency of the Fundamental (in Hz)	625	17.14	507	5.90	393	20.33
End Frequency of the Fundamental (in Hz)	563	35.00	486	6.58	336	26.70

Table 6. Results of univariate analysis of variance for the five measured variables.

Variable	Reject H_o	Level of Significance
Duration	No	
Number of Bands	No	
Start Frequency of the Fundamental	Yes	$\alpha = .005$
Mid-Point Frequency of the Fundamental	Yes	$\alpha = .005$
End Frequency of the Fundamental	Yes	$\alpha = .01$

Analyses of call duration or number of bands do not allow rejection of the null hypothesis that all of the samples could have been drawn from a single population. The results for call duration support my own impression that call duration did not vary in a systematic manner between individuals. This contrasts with the findings of Espmark (1975), Marler and Hobbett (1975), Lillehei and Snowdon (1978) and Snowdon and Cleveland (1980) that call duration can sometimes be used to distinguish between individuals.

The finding that number of bands did not distinguish individuals probably reflects the inadequacy of this measure for describing the acoustic character of this call. A comparison of Figures 37 and 38 shows that while KA has a wider spacing of bands than AN, the former shows a more even distribution of energy throughout the frequency range 0-8000 Hz so that every harmonic is seen as a visible band. The basic coo of AN (Figure 38), in contrast, shows more concentration of energy below 2000 Hz and above 4000 Hz. The middle harmonics are not emphasized and are not, therefore, counted as bands. Both animals may show about the same total number of bands but the distribution of energy differs and the calls sound very different to the ear.

In contrast to the above negative findings, all three measures of the dominant band do show greater variance between individuals than within individuals. This finding is consistent with the hypothesis that distinguishing cues exist which allow recognition of individuals.

A note of caution, however, must be added even to the above positive findings. The age-sex category chosen for analysis (adult female) may not be as uniform as assumed. It is possible that the differences noted between

individuals are really age-related differences, not markers of individuality. Several studies purporting to show individualization in call structure have age as a confounding factor (Marler and Hobbett, 1975; Lillehei and Snowdon, 1978). On the other hand, when group size is small and there are few members in each age-sex class, age-sex markers may go a long way toward specifying individual identity.

Demonstrating that sufficient structural cues exist for individual recognition of the calling animal does not in itself show that such cues are used by the recipients of the call. In order to demonstrate the latter, the usual procedure is to collect data on differential response by recipients to spontaneous vocal emissions or to playbacks of recorded calls from socially significant conspecifics (Hansen, 1976; Waser, 1977; Kaplan et al., 1978; Cheney and Seyfarth, 1980). While such procedures are useful for illuminating the functions of calls which evoke easily observable motor responses, it is much more difficult to discern the function of calls which do not have obvious, immediate effects. The basic coo of the rhesus monkey falls in this latter category. Many times there is no obvious response to its emission or at most the response may be a single antiphonal coo. Lindburg (1971) suggested that the coo given while foraging may function to establish position, allowing visually out-of-contact monkeys to remain in aural contact. While this explanation sounds plausible, it does not explain why the call may have been under selective pressure to give information about individual identity. As a supplement to the demonstration that cues pertaining to individual identity exist in this call and as an inducement to further investigation of this topic, I would like to offer an alternate explanation of the function of the basic coo.

Kummer (1971) has suggested that the social world of higher non-human primates is composed of two classes. The "few animals to which it is primarily attracted, the familiar members of its group" and the "strangers" who are avoided. Certainly, there is abundant observational and experimental evidence that rhesus groups not only avoid contact with other groups, they are also extremely aggressive toward any unfamiliar conspecific who has the misfortune to be experimentally introduced into their midst (Bernstein, 1964; Southwick, 1967; Southwick et al., 1974). What has been less well appreciated is the fact that the "stranger" is not just the animal with whom the group has never interacted; <u>it is also the animal with whom they have not recently been in contact</u>. Vessey (1971) conducted a series of removal and reintroduction experiments with individuals from groups of rhesus on two islands near La Parguera and found that reintroduced females and low-ranking males were frequently attacked and chased by other group members. An incidental result of research on mother-infant separation (conducted in laboratory colonies) has been the finding that mothers who are temporarily removed from a familiar group are frequent participants in aggressive interactions when they are returned to the group (McGinnis, 1979). At Silver Springs, as noted earlier, a major portion of the southside group left the provisioning area for a period of six months and upon their return interacted only agonistically with the remnant animals who had once been tolerated as group members (Maples, personal communication). All of these observations suggest that rhesus monkeys need continuing social interactions in order to maintain "recognition" of individual conspecifics and <u>inhibit</u> xenophobic reactions.

It is possible that the basic coo plays an important role in providing a maintenance level of individualized interaction between group members, particularly in forest-dwelling animals who are frequently out of visual contact with each other. Individualization in this sound signal, like individualization in visual appearance, may be a convenient way of reminding other group members of the continuing status of that individual as a "familiar" other (i.e., as a frequently encountered entity). Such reminders may have evolved in concert with a social system in which the familiar conspecific is tolerated and the unfamiliar one is avoided or aggressively displaced.

The above analysis and discussion can be no more than a beginning toward an understanding of the existence and function of individualization in sound signals. Further field and laboratory investigation will be necessary but it is hoped that an innovative explanation of "contact" calls may stimulate appropriate research.

CHAPTER V

ISSUES IN THE STUDY OF PRIMATE AUDITORY COMMUNICATION

The purpose of this chapter will be to place in broader perspective some of the findings presented and issues raised in earlier chapters. Where applicable, related or parallel topics in the study of human communication will be discussed. Finally, research needed to clarify specific problem areas will be suggested.

In Chapter III, I discussed the problem of providing an adequate operational definition of the basic unit of analysis, the "vocalization" or "call," and suggested that it may be useful to define this unit functionally rather than phonologically or acoustically. Burns (personal communication) has suggested a parallel here with the definition of the phoneme, the unit which Gleason (1961) has referred to as the most basic element in the expression system of any language (p. 9).

Phonemes are very short sounds, meaningless by themselves but when they are strung together they produce the meaningful units of a language, the morphemes. In any language, a single phoneme is usually not a single sound but a family of sounds. A change in phonemes is signaled only when there is a shift in <u>meaning</u> to the native speaker. Gleason (1961) has defined a phoneme by suggesting that the "smallest difference which can differentiate utterances with different contents is a difference of a single phoneme" (p. 9).

Later he goes on to state that "phonemes are not, however, any sort of physical reality discernible by instrumental techniques or direct observation. The phoneme cannot . . . be acoustically defined . . . . It is an abstraction from the psychological and acoustic patterns which enables a linguist to describe the observed repetitions of things that seem to *function* within the system as identical in spite of obvious differences" (p. 269) (italics mine). It is function, therefore, and not phonology or acoustics alone, which defines a phoneme according to Gleason.

Non-human primate vocalizations, upon first appraisal, do not seem to have much in common with human phonemes. Most are longer in length than human phonemes and they have meaning when uttered in isolation, unlike phonemes which must be strung together before they become meaningful. The meaning of a vocalization is not arbitrarily defined by convention (like that of the phoneme groupings) but seems to be relatively invariant across the species. Despite these differences, both phonemes and vocalizations are difficult to define acoustically. The success of a functional definition for delimiting phonemes should give pause to those primatologists who have advocated the exclusive use of acoustic criteria for delimiting vocalizations and eschewed all reference to function or meaning (cf. Altmann, 1962; Marler, 1965; Erwin, 1975).

One of the problems with a functional definition of the "vocalization" is the difficulty which human observers have in ascribing specific meaning or function to a particular sound sequence. However, it may not be necessary to understand the specific meaning or function of each sound unit as long as there is evidence of a *contrast* in the meaning of the two sounds units as

shown by a relatively consistent difference in the response of recipient animals. Linguists, likewise, do not necessarily need to concern themselves with a precise understanding of the actual new meaning which a phoneme shift creates in a morpheme; they merely need the testimony of a native speaker that shift in meaning has occurred.

In Chapter 3, I suggested the use of a "frequency of occurrence in isolation" criterion for determining whether a sound sequence should be considered a complete vocalization or merely part of a vocalization. In the classification of communication units, Altmann (1967) (following a suggestion by Struhsaker (1967)) has distinguished between "criteria of sequential demarcation" (which indicate how to break up the temporal continuum) and "criteria of membership" (which indicate when any two events are members of the same class). While the "frequency" criterion I have suggested is a criterion of sequential demarcation, the "contrast in meaning/function" criterion (as evidence by contrast in the response to the recipients) is a criterion of class membership. Thus, to suggest that call status should be given to any sound sequence which shows evidence of distinctive function when emitted in isolation is to satisfy both kinds of cataloging criteria. In practice, it is not always possible to discern distinctive function and one must be satisfied with distinctive form and the assumption that this distinctive form is tied to a distinctive function.

The above discussion has assumed a relatively categorical coding of information. However, rhesus vocalizations, as discussed earlier, show evidence of grading in signal form and this is usually assumed to represent and communicate corresponding gradation in motivation and message.

Altmann (1967) has called attention to the fact that analog variation in signal form has not been shown to be indicative of a corresponding "functional continuity" (i.e. of an analog variation in the underlying motivation for that signal and the communication of that information). At least some of the variability in signal form must be no more than the range of variation characteristic of any trait (no two sounds are ever precisely alike) and may be more indicative of the degree of normalizing selection that has operated on signal form than of a variation in function. One could even suggest that an animal with more highly evolved perceptual-processing equipment may be able to reliably classify an incoming sound signal into the appropriate meaning category based on fewer cues or in the face of more extraneous stimuli than is true for less evolved animals. Thus, the calls and other displays of non-human primates may be less stereotyped and less high contrast than those of most birds and fish because extreme stereotypy and high contrast in signal form are not necessary to achieve a high degree of reliability in the categorizing of the signal by recipients.

Despite these considerations, gradation in signal form is such an impressive feature of rhesus vocal communication that it deserves further investigation. Perhaps a useful first step would be to consider, as I suggested in Chapter III, that signal form can vary along any of several component form gradients. Each of these gradients of form, in turn, may be tied to a separate meaning gradient. Position along each gradient may be making a separate contribution to the meaning. It is possible that rhesus monkeys respond to some sound signals not (or not just) by categorizing them but by assessing the position of the signal along multiple structural continua, each of which may

give information about position along a motivational or semantic continuum. The "meaning" of a specific vocalization may be at least partly the result of the convergence of effects wrought by position along multiple form-meaning continua.

This is not to suggest that categorical meaning does not also occur in rhesus calls. Some of the calls, as noted in Chapter III, are highly stereotyped in form and evoke stereotypic responses. Even for those calls which grade into one another in form and response, the synthesized call (the result of position along multiple form gradients) may mean something over and above the product of position along contributing meaning gradients. To the degree that the whole means something more than the sum of its "parts," one could suggest that a certain degree of categorization may co-exist with a certain degree of functional analog variation in "graded" sound signals. That such a co-existence is not beyond the realm of possibility is shown by the fact that human speech is characterized by both digital and analog coding of information (Sebeok, 1962).

Despite the more obvious categorical meaning of sound signals which we human observers seem prone to attend to, it seems useful to at least explore the possibility that change along a single form gradient may make a consistent contribution to change in meaning which can be seen across many "types" of sound signals. Most human observers already assume this to be true along a volume gradient (louder screams signal more intense fear than softer ones, louder threats signal more intense rage, etc.), but there may be other form-meaning continua which can be established. Some of the technology for carrying out this kind of research has already been developed by researchers

exploring human speech perception. Using the Pattern Playback Synthesizer developed by Franklin Cooper (which works on the reverse principle of the spectrograph), it has been possible to artificially construct (and systematically modify) a two-dimensional visual image which can be translated by the synthesizer into a sound. The advent of computer-controlled synthesizers promises even greater precision for this kind of research (see Zoloth et al., 1980 for one prototype). Using such devices, it should be possible to experimentally vary sound signal form along one structural gradient at a time and observe any change in meaning for recipients (as measured by change in response).

The possibility that a series of form-meaning gradients may be accessed in the production and reception of an individual sound signal suggests that it may be useful to re-evaluate Hockett's concept of "blending" and its role in the origin of speech. Hockett has suggested that the "closed" call system of non-human primates evolved into the "open" vocal communication system of humans with the "production, under circumstances appropriate for two different calls . . . of a call . . . that has some features of each (Hockett, personal communication; also Hockett and Ascher, 1964). Hockett's description of the intial impetus for change in the direction of human speech may be built on an inadequate conceptualization of non-human primate vocal communication and our understanding of how the shift toward human speech was effected may likewise be inaccurate. If we move away from the one call = one meaning conceptualization of primate calls and move toward the perspective that a limited number of form-meaning gradients are involved in the production (and decoding) of a large number of calls, then

there may be a sense in which the vocal communication systems of non-human primates already show evidence of "openness" and "blending." However, it is a blending of analogically coded information. Perhaps it is to the blending of categorically coded information that we should look for the beginnings of human uniqueness. Indeed, Hockett and Ascher's description of "blending" takes on new meaning if we add this additional requirement. A more refined understanding of the nature of non-human primate vocal communication can help us to speculate with greater precision about the changes necessary to evolve human speech.

In an interesting experiment on the neuroethology of squirrel monkey vocalizations, Juergens (1979) sorted a large sample of squirrel monkey calls into a small number of classes of continuously varying but similar form. He suggested that the continua of form which these five classes encompassed "expressed shades of more general motivational states" (p. 88). He tested one dimension of this motivational state, its hedonic value to the animal, by placing electrode-implanted animals in a self-stimulation experiment in which they could switch on and off electrical simulation to vocalization-eliciting brain loci. Using this procedure, he was able to establish the following form-aversiveness principles:

1. For all calls, "an increase in the aversiveness of the emotional state underlying a call is generally paralleled by an increase in total frequency range and intensity."

2. Among harmonic calls, "higher-pitched variants are more aversive than the lower-pitched."

3. Among harmonic calls, "irregular frequency course is more aversive than a smooth one."

4. Among harmonic calls, "constant or descending frequency course is more aversive than an upward shift of frequency."

Juergens' success in establishing a relationship between change in the form of a sound signal and change in one aspect of motivation provides support for the idea being developed in this section that there may exist form-meaning gradients which contribute to multiple calls. Although motivation is not necessarily congruous with meaning (how much of the signaler's motivational state is actually communicated can only be assessed by examining the response of recipients of the signal), still this kind of research gives a strong basis for inferring form-meaning continua in this species.

It would be interesting to see if some of the principles of form-aversiveness which Juergens established for squirrel monkeys also apply to the sound signals of other non-human primates. In a literature review which transcended not only species and orders but even classes of vertebrates, Morton (1977) surveyed the evidence in support of a generalization first suggested by Collias (1960). This was that harsh, low-frequency sound signals are associated with hostile behavior and high-frequency, tonal sound signals with fright, appeasement or friendly approach. Morton concluded that there exist "motivation structural rules (MS) governing the physical structure of close contact sounds in animal communication systems" (p. 855). He suggested that not only are aggressive sounds consistently harsh, low frequency sounds and submissive sounds relatively tonal and high-frequency in a wide variety of birds and animals, he also proposed a number of other form-motivation regularities relevant to the starting frequency, the change in frequency, the degree of harshness and the amount of grading in specific

calls. While definitive support for these proposals remains to be amassed, the possible existence of metaprinciples of form-meaning which can be applied across taxa as broad as classes is intriguing and provides further incentive for investigating form-meaning correlation both within and between species.

The search for support may find glaring exceptions as well as validating examples of such general rules. This is certainly the case with respect to the harsh, low-frequency "basic grunt"used by rhesus monkeys in friendly contexts. Not only does this call violate Morton's generalization that such calls should be high-frequency and tonal, it also converges in form with another rhesus call, the trilled "one-unit pant threat" used in agonistic contexts. The similarity between these two calls is so great that it is impossible to define acoustic criteria which can be used to sort spectrograms of these calls. Yet, the monkeys react very differently to these two sounds. In accordance with the functional definition of a call outlined earlier, I have classified these sounds as two different calls despite their acoustic similarity.

It is possible that the calls are phonologically identical and that recipients use contextual cues to distinguish the signaler's motivational state (just as humans use contextual cues when interpreting the meaning of a linguistic utterance). However, there exists experimental evidence that another cercopithecid species, the vervet monkey (Cercopithecus aethiops), is able to use subtle acoustic (and context-free) cues to distinguish between grunts which to the human observer (and to superficial spectrographic analysis) appear to be identical (Cheney and Seyfarth, 1982). This suggests a highly evolved perceptual-processing system in these animals (a feature also indicated by Green's (1972, 1975) study of Macaca fuscata coo calls). The

ability to attune to very fine-grained differences in signal form may have evolved in concert with subtle distinctions in signal form as a means of increasing the information which could be conveyed in the auditory channel. Finer-grained analysis of both the acoustic form of rhesus grunts and the responses they evoke would seem to be a fruitful area for future research.

The possibility that subtle acoustic differences may distinguish similar-sounding calls provides more, not less, justification for the use of a functional criterion for constructing a taxonomy of calls. To the degree that human observers have neither the sensory nor the instrumental apparatus to distinguish these acoustic differences, a functional criterion may be an essential tool for analyzing the vocal repertoire of any species.

The analogy introduced at the beginning of this chapter may again prove instructive. Although most field linguists depend on a functional definition of the phoneme when actually cataloguing the phonemes of a language, there is one theoretical school (represented by the intellectual line of Leonard Bloomfield, Roman Jakobson, C.G.M. Fant and Morris Halle) which suggests that a phoneme can best be defined as "a distinctive feature or set of features, irrespective of the presence or absence of other features" (Chao, 1970, p. 36). While this definition contradicts Gleason's assertion (quoted earlier) that phonemes do not have a "physical reality" (1961, p. 269), it still requires reference to function when setting up the class whose members will then be examined for a common feature.

Finally, it seems useful, in this overview of issues raised in earlier chapters, to extend the discussion of individualization in coo calls initiated in Chapter 4. Individualization of sound signals, as noted in Chapter 1, has not

received much attention by mammalogists. Primatologists are only beginning to document its existence and explore its functions in non-human primates. Since auditory communication in its linguistic form occupies a salient position in the social behavior of humans, its functions have been an object of attention for many years. It is not surprising, therefore, that it was a social anthropologist who in 1923 first suggested that one of the functions of human speech may be to establish "ties of union . . . created by a mere exchange of words" and called this phenomenom "phatic communion" (Malinowski, 1923). In discussing this phenomenom, Sebeok (1962) quotes a greeting card legend which reads "This card serves no useful purpose--except to make money for the manufacturer and to assist me in communicating with you and sustaining our relationship" (italics mine). It is exactly this latter function which I suggested for the rhesus basic coo in Chapter IV. The use of words to maintain social bonds may have a non-linguistic but auditory antecedent.

The necessary and sufficient conditions for establishing and maintaining individual bonds in socially living animals are still poorly understood (see Rajecki, et al., 1978 for a comprehensive theoretical review). Elsewhere I have suggested, following Cairns (1966), that mere proximity (with its concommitant opportunities for sensory exchange) may be sufficient to result in attachment bonds between susceptible animals and that the emotional-motivational infrastructure underlying these bonds may also manifest itself in the altruistic behavior which is usually cited as evidence of "kin recognition" (Peters, in press). What has never been systematically investigated (despite the plethora of research on mother-infant attachment) is the specific role of vocal communication for producing and sustaining bonds. If, as I suggested in

Chapter I, we wish to improve our understanding of the proximate causes of social organization, this would seem to be an area with interesting research potential. While communication acts in all the modalities may function as social cement, vocal communication has the specific advantage of not requiring close spatial proximity. Considering the degree to which foraging competition may serve as a major centrifugal force in socially living animals, it does not seem unreasonable to hypothesize that certain vocal sounds may have evolved specifically to serve as a substitute for spatial proximity in maintaining social bonds.

The large number of related problems and new perspectives generated by the present attempt to describe vocal communication in the rhesus monkeys of Silver Springs may have its own lesson. Describing sound signals may seem to the uninitiated to be a relatively simple process of setting up categories, sorting samples and ascribing meaning to the types. In practice, as the preceding analysis has indicated, it may involve enormous wrestling with procedural and theoretical issues. Research is often undertaken to test hypotheses generated by theory. Yet, the degree to which "mere description" also serves to generate new concepts, methods and theoretical perspectives should not be undervalued.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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